The movement ecology of common bream *Abramis brama* in a highly connected wetland using acoustic telemetry

Emily R. Winter

Thesis submitted in partial fulfilment of the requirements of the degree of Doctor of Philosophy

Bournemouth University

Supervisors: Prof J. Robert Britton & Prof. Genoveva Esteban

October 2020

Blank page

Abstract

Evidence increasingly suggests that the movement behaviours of potamodromous fishes can be highly diverse in well-connected systems. Intra-population divergence in spatial and temporal resource-use is an important component of fish distribution patterns and population structure, which can affect population viability and adaptive potential. The common bream *Abramis brama* ('bream') is a potentially strong model species for testing the importance of habitat connectivity and examining variation in movement patterns in lowland rivers. Concurrently, the Broads National Park ('Broads'), eastern England, provides a large network of interconnected rivers, lakes and dykes in which to examine unconstrained fish movement. Thus, biotelemetry was applied to investigating the movement ecology of bream in the northern Broads wetland system.

Acoustic telemetry is a central tool for fish movement ecology, but robust data interpretation requires detailed knowledge of its efficiency and the fate of tagged individuals. Here, variation in acoustic receiver performance was quantified, along with the post-tagging survival rates of bream and Northern pike *Esox lucius*. The results demonstrated that acoustic detection range and efficiency were highly variable temporally, being negatively impacted by increased water temperature and precipitation, or reduced transparency (a surrogate measure of algal density). For both bream and pike, post-tagging survival rates were lowest in the reproductive periods of both species, but in bream, fish tagged just prior to spawning actually had the highest subsequent survival rates. Acoustic signal loss, potentially due to tag expulsion, also accounted for the loss of some bream from the study. These results emphasise the need for long-term receiver monitoring and consideration of the relative effects of tagging to be incorporated into telemetry study design.

Geostatistical models of stable isotope landscapes ('isoscapes') provide a complementary tool to telemetry for assessing and predicting animal movements. The efficacy of single versus dual-isotope isoscapes in predicting the foraging locations of roach *Rutilus rutilus* was compared, with the dual-isoscape approach emerging as the most efficient. Dual-isoscapes were then applied to predicting the movement distances of individual bream in comparison to their movements recorded

by acoustic telemetry. This revealed that isoscape-predicted movement was a significant predictor of the spatial extent of subsequent movements recorded by telemetry, suggesting repeatable individual activity levels between years. Dual-isotope isoscapes can thus provide a reliable alternative or complementary method to telemetry.

Acoustic telemetry was then applied to investigating the diversity of bream migration behaviour throughout the northern Broads wetland system and examining more fine-scale spatial and social preferences during their reproductive period, with the aim to understand their spatial occupancy patterns and spatial population structure. Bream movements showed considerable diversity, with some individuals making repeatable spawning migrations of up to ~25 km, whereas others were relatively sedentary. Behavioural type (resident/ migrant) was highly consistent within individuals, although both phenotypes were detected mixing in space and time during the reproductive period. This suggests the Broads bream population is comprised of several distinct, semi-independent subpopulations that reside in spatially distinct areas throughout much of the year, but converge and potentially interbreed in their spawning period.

Thus, this research explores the utility of acoustic telemetry and stable isotope tracking for documenting the movement ecology of lowland wetland fishes. The results emphasise the fundamental importance of connectivity in freshwater systems for enabling and maintaining high phenotypic diversity in the migration behaviours of potamodromous fishes.

Table of Contents

List of Figures

List of Tables

Acknowledgements

First and foremost, I would like to thank my supervisor, Prof Robert Britton, who has provided unwavering support throughout this project, including expert help, knowledge and advice, not only academically, but also practically in the field and regarding professional development. Much of this was achieved while working remotely, and for that I am extremely grateful. I would also like to thank all members of the PhD Steering Group, but particularly Rory Sanderson (Environment Agency) and Stephen Rothera (Natural England), for their regular supervision and guidance, and for facilitating multiple opportunities for public engagement.

I am indebted to Steve Lane (EA) and Andy Hindes (Fishtrack Ltd) for their endless inspiration and advice on manuscript development. Also, to them, Kevin Grout (EA) and many others at the Environment Agency and beyond who joined me in the field, thank you for providing invaluable assistance, for enduring long hours and for making the project a truly enjoyable experience. Thanks also to the local angling community for their considerable voluntary support with fish sampling.

I am grateful for the support and advice from other academics and students at Bournemouth University, especially my second supervisor, Prof Genoveva Esteban, who introduced me to the SAMARCH project, and Vicky Dominguez Almela, Pete Davies, Dr Catie Gutmann Roberts and Dr Emma Nolan, who helped with data analyses and answered my many questions. I also wish to acknowledge Hugo Flávio (DTU, Denmark) for his personal assistance with deciphering the *Actel* package in R. Also, to the anonymous reviewers, thank you for your comments and contributions that have greatly improved the quality of the publications resulting from this project.

Finally, thanks go to my friends and family for their tireless encouragement and belief throughout the completion of this project.

The financial support of Bournemouth University and of the EU LIFE+ Nature and Biodiversity Programme: LIFE14NAT/UK/000054 is gratefully acknowledged, as is funding and resource support from the Environment Agency.

Author's declaration

I (ERW) confirm that the research presented within this thesis is my own.

The following research papers were, however, published or prepared for publication in collaboration with Andrew M. Hindes (AMH), Steve Lane (SL) and J. Robert Britton (JRB). In all cases, ERW, AMH, SL and JRB conceived the ideas, designed methodology and collected the data, and ERW analysed the data and led the writing of the manuscript:

Winter, E. R., Hindes, A. M., Lane, S. and Britton, J. B. High temporal and spatial variability in the detection efficiency of acoustic telemetry receivers in a connected wetland system. *Hydrobiologia* (submitted July 2020; in review; Chapter 2).

Winter, E. R., Hindes, A. M., Lane, S. and Britton, J. B. 2020. Predicting the factors influencing the inter- and intra-specific survival rates of riverine fishes implanted with acoustic transmitters. *Journal of Fish Biology,* 97 (4), 1209-1219. (Chapter 3)

Winter, E. R., Hindes, A. M., Lane, S. and Britton, J. B. Dual-isotope isoscapes for predicting the scale of fish movements in lowland rivers. *Ecosphere* (submitted March 2020; in revision; Chapter 4).

Winter, E. R., Hindes, A. M., Lane, S. and Britton, J. B. Movements of common bream *Abramis brama* in a highly-connected, lowland wetland reveal spatially discrete sub-populations with diverse migration strategies. *Freshwater Biology* (submitted September 2020; in review; Chapter 5).

Winter, E. R., Hindes, A. M., Lane, S. and Britton, J. B. Acoustic telemetry reveals strong spatial preferences and mixing during successive spawning periods in a partially migratory common bream population. *Aquatic Sciences* (submitted October 2020; in review; Chapter 6).

Blank page

1 Introduction

1.1 Overview

This first chapter outlines the main themes of the thesis: habitat connectivity and the applicability of acoustic biotelemetry to monitoring animal movements in the aquatic environment. The study species, study system, and aims and objectives are then introduced. The thesis is presented in an integrated format, whereby material is incorporated in a style suitable for submission and publication in a peer-reviewed journal. Thus, the data chapters (Chapters 2 to 6) are each presented as original and complete pieces of research, either as the actual, published paper or as a manuscript under review. This format has been chosen as it provides flexibility around the types and numbers of papers included in the thesis. Finally, Chapter 7 discusses the implications of this research and concludes the thesis. A complete list of references is provided at the end, in order to avoid their replication in the chapters and to improve readability.

1.2 The ecological importance of habitat connectivity

Connectivity within and between ecosystems allows organisms, energy and information to flow across landscapes. In promoting structural and biological diversity, and enhancing the resilience of ecosystems to disturbance, this is of fundamental importance to ecological integrity (Massol et al. 2011, Correa Ayram et al. 2016). Connected ecosystems function as linked elements of a mosaic of habitats; their area, quality and spatial distribution are key to population viability through driving organism dispersal, growth and survival (Hodgson et al. 2011). Thus, connectivity has become a key consideration in environmental conservation and restoration across terrestrial, marine and freshwater realms (Correa Ayram et al. 2016, Olds et al. 2016).

The importance of space for the movement and dispersal of organisms has long been recognised (e.g. MacArthur and Wilson 1967). Where a single habitat cannot deliver all essential resources for the completion of a life cycle, it is vital that animals are

able to move between habitats (Dingle 1996). Indeed, habitats are themselves dynamic and their suitability may fluctuate temporally (Pickett and White 1985). In response, animal movement may occur at a range of spatial scales, from diel microhabitat shifts (e.g. Armstrong et al. 2013) to seasonal migrations across biomes (Berthold 1988, Brower 1996, Klemetsen et al. 2003, Pomilla and Rosenbaum 2005). In freshwaters, longitudinal connectivity is important for diadromous species that utilise both marine and freshwater environments. These include anadromous salmonids (e.g. *Salmo salar*, Klemetsen et al. 2003), lampreys (e.g. *Lampetra fluviatilis*, Tummers et al. 2016) and shad (e.g. *Alosa fallax*, Davies et al. 2020) that, as juveniles, migrate from rivers to the sea for growth and maturation before their return as adults to headwater streams for reproduction. Beyond these relatively predictable migrations, the dispersal of all organisms among ecosystems is dependent on connectivity, with even the presence of wind-dispersed plants being positively impacted by habitat corridors (Damschen et al. 2014). This is important for the recolonization of habitats following natural and anthropogenic disturbances (MacArthur and Wilson 1967, Pickett and White 1985), as isolated habitats typically show reduced or slowed colonization (Trekels et al. 2011, Helsen et al. 2013). Ultimately, the capacity for movement and dispersal of organisms defines the size and structure of metapopulations, and underpins their persistence over evolutionary timescales (Correa Ayram et al. 2016).

Vagile organisms connect ecosystems across the globe and, in transferring energy and manipulating trophic dynamics, their influence on ecological networks can be widespread (Massol et al. 2011). Thus, their presence or absence can have cascading effects on ecosystem functioning and drive transitions between alternative stable states (Massol et al. 2011, Bauer and Hoye 2014). For example, anadromous fishes transport marine-derived nutrients to headwater streams, altering nutrient cycling and productivity (Childress et al. 2014), and in wetlands, the overwintering migration of fish into tributaries affects both plankton dynamics and predator foraging ecology, with consequences for lake turbidity (Hansson et al. 2007, Brodersen et al. 2011, Hansen et al. 2019b). Moreover, the integration of spatial and trophic ecology drives both food-web complexity and stability, with a recent study attributing global biodiversity loss to the loss of biomass and energy during the dispersal of organisms

over habitat fragments (Ryser et al. 2019). Understanding the functional ecology of movement and dispersal across connected systems is therefore fundamental to successful habitat management, including efforts to prevent, reduce or mitigate the effects of fragmentation (Massol et al. 2011, Bauer and Hoye 2014).

The concept of connectivity can also be applied to patterns of gene flow, which offer insight into the extent of population dispersal (Klinga et al. 2019). The separation of populations by physical or physiological barriers causes reproductive isolation, restricting the transfer of genetic information and potentially leading to their genetic differentiation (Adams et al. 2016), even at relatively small spatial scales (Rodger et al. 2020). In the event of disturbance, such as a disease outbreak, the rate of gene flow between populations is positively related to their resilience, with connected populations showing greater evolutionary potential (Jousimo et al. 2014, Christie and Knowles 2015). For example, the ability of ash *Fraxinus excelsior* trees to adapt and recover from ongoing ash dieback will reportedly depend on the rate of transfer of genetic resistance across European landscapes (Semizer-Cuming et al. 2017). Spatial genetic screening can thus provide a preliminary assessment of population connectivity and be used to direct conservation efforts (Klinga et al. 2019).

Connectivity is key to the provisioning of ecosystem services (Correa Ayram et al. 2016) and, upon this realisation, as early as the 19th century (Francis 1870), humans have taken considerable actions to reconnect fragmented habitats. This has involved installing road bridges (Weston et al. 2011) and fish passes (Figure 1.1; Silva et al. 2018), removing fences (Dupuis-Desormeaux et al. 2018) and dams (Magilligan et al. 2016), and restoring habitat corridors (Shepherd and Whittington 2006). Freshwater systems comprise only a fraction of the Earth's surface (~0.8 %) and, in contrast to marine or terrestrial ecosystems, their predominantly hierarchical, dendritic nature amplifies the effects of artificial barriers (Fagan 2002). However, where structures in these systems are removed, or fishways installed, potamodromous and diadromous fishes can naturally recolonize upstream habitats (Pess et al. 2014, Benitez et al. 2018). In addition, the lateral reconnection of floodplains and mainstem rivers can enhance the diversity of fauna and flora (Pander et al. 2018), and promote the retention of excess nitrogen and phosphorus, reducing

eutrophication (Newcomer Johnson et al. 2016). Instream barriers continue to be removed at an increasing rate in more affluent regions of the world (American Rivers 2019), however in countries with emerging economies, the burgeoning construction of major hydropower dams is likely to further reduce the global number of free-flowing rivers by ~20 % (Zarfl et al. 2015). Consequently, there remains a need for mitigation of the ecological impacts of fragmentation in rivers (Zarfl et al. 2015), and habitats more widely (Correa Ayram et al. 2016).

In an increasingly anthropogenic world, habitat connectivity may not always confer an advantage to ecosystems, instead enhancing vulnerability to stressors, such as invasive species or pollution (Leuven et al. 2009). This is particularly evident on islands, where the introduction of alien predators has led to higher rates of extinction of birds and mammals than experienced on continents (Loehle and Eschenbach 2012). Consequently, in aquatic systems, intentional habitat fragmentation has been suggested as a potential management practice to limit species invasions and conserve ecological integrity (Rahel 2013). An example is the isolation of eutrophic wetland lakes as part of their biomanipulation, allowing the fish community to be modified (such as the removal of zooplanktivorous fishes, which increases algal grazing rates) to promote the restoration of clear-water, macrophyte-dominated states (e.g. Moss et al. 1996). However, human interventions in ecology can have unintended consequences (e.g. Takekawa et al. 2015) and reconciling the preservation of movement and dispersal for some species, with the blockage of passage for others, remains a challenge (Rahel and McLaughlin 2018).

Figure 1.1: Powick weir and fish pass on the lower River Teme, Severn catchment, western England. The weir was partially removed in 2018. Photographs courtesy of Dr Andrew Harrison and Dr Catherine Gutmann Roberts (Bournemouth University).

1.3 Aquatic acoustic biotelemetry

In aquatic environments, the ability to directly observe animal behaviour is highly challenging. However, the electronic tagging of aquatic animals has developed sufficiently to enable indirect measurements of animal movements that can be related to their behavioural ecology (Hussey et al. 2015). Acoustic biotelemetry ('telemetry') provides one of the most versatile methods to track animal movements in both freshwater and marine environments (Crossin et al. 2017), and consequently, its use has grown exponentially in recent decades (Hussey et al. 2015).

Acoustic transmitters ('tags'; Figure 1.2) emit ultrasonic coded signals that can be detected by submerged hydrophones and receivers ('receivers'; Figure 1.3). Tags are either surgically implanted into the study organism (most common), or externally attached or inserted into the gastrointestinal tract (Crossin et al. 2017). Receivers can be manually operated, involving actively locating and following certain individuals (Stasko and Pincock 1977), or automated, involving continuous passive 'listening' at fixed locations (Klimley et al. 1998). The most optimal arrangement of stationary receivers depends on the study system and the research aims, however possibilities include gates, curtains or arrays (Heupel et al. 2006). Upon detection, a receiver logs the tag's unique identity code along with a date-time stamp. This information can then be accumulated across space and time to produce animal movement tracks. Recent advances in acoustic telemetry have facilitated opportunities to track animals across spatial scales ranging from <5 m to thousands of kilometres, across temporal scales ranging from days to years (Donaldson et al. 2014), and for species or life stages as small as 10 g (juvenile Chinook salmon *Oncorhynchus tshawytscha*; McMichael et al. 2010) and as large as 20 tons (whale shark *Rhincodon typus*; Cagua et al. 2015). Much of the technological development has been in miniaturising tags and extending their battery lives, allowing for a greater diversity in study species (e.g. to include Anguillids and flatfish; Thorstad et al. 2013, Neves et al. 2018), along with longer and more reliable deployments (Hussey et al. 2015). Concurrently, affordability of the technology has also improved, leading to larger sample sizes and even multi-species studies (e.g. Taylor et al. 2018). Thus, acoustic telemetry has

many applications, including in fisheries stock assessments, managing habitats and monitoring invasive species (Crossin et al. 2017).

Acoustic telemetry is highly effective at assessing the two-dimensional (horizontal) space-use of aquatic animals, but understanding movement in three-dimensions or how it relates to animal physiology, foraging or social behaviour has required further innovation. Transmitters equipped with sensors (e.g. depth, acceleration, temperature) can provide information on the tagged animal's internal and external environment (Donaldson et al. 2014), while the pairing of acoustic telemetry with biological markers, such as genetics, inorganic trace elements or stable isotopes (SI), can empirically link animal movement to population structure or trophic ecology (Hussey et al. 2015). This has been successfully demonstrated in studies on lemon sharks *Negaprion brevirostris* (Kessel et al. 2014a) and burbot *Lota lota* (Harrison et al. 2017), among others. Telemetry has also played a valuable role in validating the 'isoscape' tracking of animals, in which geostatistical models of isotopic landscapes are used to calculate spatially explicit probabilities of origin for animal tissue samples (Vander Zanden et al. 2018). In the aquatic environment, applications have focussed on the coupling of oceanic isoscapes with the satellite telemetry of sea turtles (Seminoff et al. 2012, Vander Zanden et al. 2015a, Bradshaw et al. 2017). The method assumes high site fidelity of tagged animals, in order for SI samples collected at the time of tagging to reflect subsequent movements recorded by telemetry (Bradshaw et al. 2017), except where the recapture of tracked animals is possible (Pearson et al. 2020). Yet, few alternative tracking techniques offer the level of accuracy and precision awarded by electronic telemetry technology (Vander Zanden et al. 2018, Coffee et al. 2020). The complementary use of telemetry and other biological measures therefore provides strong opportunities for exploring the functional ecology of animal movements (Hussey et al. 2015).

Figure 1.2. Example of an acoustic transmitter (Vemco, V13) that can be implanted into fish to track their movements. Photograph taken on 10/01/2019.

Figure 1.3. An acoustic receiver (Vemco, VR2W) that monitors and records fish detections, moored onto a wooden post in the River Bure system of the Broads National Park, eastern England. Photograph taken on 16/07/2020.

The coupling of acoustic telemetry with other electronic tracking methods, such as satellite or passive integrated transponder (PIT) tags, provides an opportunity to monitor animal movements at varying spatial scales (Braun et al. 2015, Tummers et al. 2016). PIT tags are the smallest type of electronic tag and employ microchip technology that does not require an internal source of power, thus have a theoretically infinite lifespan. If implanted correctly, PIT tags provide a fast and reliable form of individual identification for an animal's entire lifetime (Lucas and Baras 2000). This has proved extremely valuable in the identification of recaptured fish during successive tagging events and in assessing the effects of acoustic tagging in some species (e.g. Ammann et al. 2013). Automated PIT tag recording systems can also be used to monitor animal movements in the field, although the detection range is usually low (<1 m) and their suitability is restricted to small river channels or monitoring fine-scale habitat use (e.g. Winter et al. 2016). Nevertheless, acoustic telemetry can be inappropriate for tracking animals in confined areas, due to insufficient spatial and temporal resolution, and so when used in tandem with PIT telemetry, the two tracking technologies can broaden the scope of studies on fish movements (Tummers et al. 2016).

The reliability of acoustic telemetry has contributed to its use in increasingly diverse environments, from rivers in the Amazon (Hahn et al. 2019) to under ice in the Arctic (Kessel et al. 2016), although few studies actually assess its performance across environmental gradients (Kessel et al. 2014b). Despite relatively high tracking precision and accuracy, evidence has shown that detection efficiency (the proportion of acoustic signals that are detected within a set period) decreases with distance from a receiver and that detection ranges (distance over which signals are detectable) fluctuate according to tag properties and environmental variables (Brownscombe et al. 2020). Failure to account for these inconsistencies risks misinterpretation of telemetry data, as indicated by Payne et al. (2010), who showed that the fluctuating detection frequency of cuttlefish *Sepia apama* was more likely attributed to variable acoustic interference with biotic noise than to their movement and activity patterns. Moreover, knowledge of receiver performance is important for study design, particularly when positioning receivers in gates, grids or curtains, and ensuring detection ranges overlap each other and/or cover all the focal habitats (Brownscombe

et al. 2019). Although assessments conducted at the start of a tracking study could therefore inform receiver deployment, long-term monitoring of detection range throughout data collection is often more robust, but is currently lacking in many acoustic telemetry studies (Brownscombe et al. 2020).

The shift towards automated, passive acoustic telemetry has led to the accumulation of large datasets from across wide spatial areas that require advanced processing and statistical analysis techniques (Whoriskey et al. 2019). The custom-made packages *VTrack* (Campbell et al. 2012), *glatos* (Holbrook et al. 2020) and *actel* (Flávio 2020) in R (R Core Team 2020) provide high-quality data visualisation and management, while dedicated online platforms facilitate the sharing of data among international collaborators (oceantrackingnetwork.org, europeantrackingnetwork.org). Only recently have attempts been made to standardise the calculation of movement metrics and guide researchers through statistical analyses (Udyawer et al. 2018, Whoriskey et al. 2019). Common approaches include generalised modelling, survival (time-to-event) analysis, mark-recapture models and network analysis, although ultimately, data interpretation is study- and species-specific (Whoriskey et al. 2019). This thesis will apply some of these methods, along with exploring other techniques, such as the use of multi-state Markov modelling (Jackson 2011).

1.4 The focal study species: Common bream *Abramis brama*

The common bream *Abramis brama* (Figure 1.4) is a large-bodied cyprinid fish native to Europe and western Asia (Backiel and Zawisza 1968). Bream are a shoaling species, favouring slow-flowing lowland habitats, where juveniles tend to be planktivorous and adults are principally benthic feeders on invertebrates such as chironomid larvae (Schulz and Berg 1987). With deep bodies and strong lateral compression, adults can grow to more than 500 mm in length and live for at least 20 years (Backiel and Zawisza 1968, Kennedy and Fitzmaurice 1968). Reproductive periods occur in spring or early summer (April – June), during which males develop raised tubercles on the head and dorsal surface of the body (Figure 1.4). Across their geographic range, bream spawning takes place at temperatures between 12 and 27 °C, although most commonly occurs between 16 and 18 °C (Backiel and Zawisza

1968). Optimal spawning substrata include submerged macrophytes, (e.g. *Myriophyllum sp.*, *Chara sp.*) and roots (Backiel and Zawisza 1968, Pinder 1997).

Bream are potamodromous, with the capacity for migration over large distances (at least 60 km), particularly during spring spawning periods (Lucas and Baras 2001, Gardner et al. 2013). The extent of their migratory behaviour appears site-specific, with some populations showing pronounced spring and autumn peaks of movement activity, while others remain largely resident year-round (Backiel and Zawisza 1968). Moreover, within populations, individual behaviour (residency or migration) can be variable (Schulz and Berg 1987, Brodersen et al. 2019) and spawning aggregations may subsequently break down into subgroups with varying migratory tendencies (Whelan 1983). Habitat use of bream changes ontogenetically (Molls 1999), with smaller, juvenile individuals seeking refuge in tributaries, boatyards or among submerged macrophytes due to their relatively high risk of predation (Broads Authority 2010, Skov et al. 2011). As larger bream (> 300 mm) are generally less vulnerable to predation (Backiel and Zawisza 1968), they are more likely found in open water habitat in large, dense aggregations, especially during winter.

Figure 1.4 Common bream *Abramis brama* caught from the River Bure system of the Broads National Park, eastern England. Spawning tubercules on the head and shoulders indicate this individual is a male. Photograph taken on 20/04/2018.

The common bream is an ecosystem engineer, playing an important role in maintaining lake systems, or shifting them towards, turbid eutrophic states (Breukelaar et al. 1994, Hansen et al. 2019a). This occurs through resuspension of the sediment and the release of nutrients during their benthic foraging, which reduces light penetration, promotes algal growth and limits the development of aquatic macrophytes (Zambrano et al. 2001, Volta et al. 2013). Additional predation on zooplankton, particularly by juveniles, leads to reduced grazing pressure on phytoplankton, enhancing the density of algal blooms (Hansen et al. 2019a). Consequently, restoration efforts in some confined systems have targeted the species for removal (biomanipulation) (Chapter 1.2; Moss et al. 1996). In general, the removal of bream (and other cyprinids) results in increased water transparency due to increased algal grazing by zooplankton, enabling a greater density of macrophytes to develop in the short-term. However, the maintenance of clear-water lakes in the long-term (> 10 years) relies on repeated removals of both fish and nutrient-rich sediment to target both top-down and bottom-up trophic processes (Van De Bund and Van Donk 2002, Søndergaard et al. 2008, Jurajda et al. 2016).

1.5 The study system: The Broads National Park, eastern England

The Broads National Park ('the Broads'), in Norfolk and Suffolk, eastern England, comprises a network of rivers, dykes, shallow lakes (flooded medieval peat diggings termed 'Broads'), fen and marshland (Figure 1.5) and is a wetland of significant ecological importance, with conservation designations for protection including Sites of Special Scientific Interest, National Nature Reserves, Special Area of Conservation and Ramsar Wetland (Natural England 2020). The wetland has remained largely free of physical barriers to fish movement since the 14th century, and therefore the northern area of the Norfolk Broads, comprising the River Bure and its tributaries the Ant and Thurne, plus associated lateral connections, provides a strong model system in which to study unconstrained fish movement. The system supports a fish assemblage that is dominated by bream and roach *Rutilus rutilus*, but also includes rudd *Scardinius erythrophthalmus*, tench *Tinca tinca*, eel *Anguilla anguilla*, perch *Perca fluviatilis* and pike *Esox lucius*. It is renowned nationally for the high quality of its catch-and-release angling for bream (e.g. multiple catches) and

pike (individual specimens to over 18 kg) (BASG 2013). Angling has been estimated to input over £100M per annum to the local economy and the fish communities upon which this depends are considered an important socio-economic resource (BASG 2018).

The Broads system is, however, not without its physiological stressors for freshwater fishes. The landscape is generally flat and the catchment is tidal for approximately 45 km inland, experiencing influxes of salt water (up to 50,000 μS cm^{-1} or > 30 PSU at ~10 km inland) during tidal surges or low river flows (Clarke 1990). Additionally, blooms of *Prymnesium parvum*, a toxic algal species, are repeatedly documented in brackish reaches of the catchment (Holdway et al. 1978). Both saline intrusion and *P. parvum* have led to dramatic fish kills in recent years (BBC 2014, ITV 2015). Furthermore, aquatic restoration efforts have involved the biomanipulation of eutrophic lakes requiring, in some cases, their disconnection from the wetland system and the deliberate removal of planktivorous and benthivorous fishes (such as bream and roach) (Chapters 1.2 & 1.4; Moss et al. 1996, Tomlinson et al. 2002). Yet, empirical assessments of fish movement ecology throughout the Bure system are limited (Jordan and Wortley 1985, Broads Authority 2010), except where this concerns fine-scale movement and responses to biomanipulation schemes (e.g. Perrow et al. 1999).

Ultimately, understanding the ecological consequences of habitat fragmentation and degradation cannot be achieved without prior knowledge of historical ecology in connected systems (Humphries and Winemiller 2009). Similarly, knowledge of optimal movement and habitat use of fishes in connected systems is crucial for informing management efforts to prevent, reduce or mitigate the effects of habitat loss elsewhere (Kärgenberg et al. 2020). Failure to consider these conditions risks the shifting of acceptable baselines and targets for restoration (Humphries and Winemiller 2009). In English waterways, there are an average of 0.75 barriers/km (Jones et al. 2019), therefore investigating fish movement ecology in the remaining connected lowland river habitats should provide fundamental insights for strengthening future conservation and restoration efforts of fragmented systems.

Figure 1.5 Scenes and habitats in the Broads National Park; (a) River Bure near Horning, (b) shallow lake (Hoveton Great Broad), (c) wet woodland (near Decoy Broad) and (d) reed-fringed marshland (Catfield Dyke, Thurne catchment). Photographs taken between 01/12/2017 and 16/07/2020.

1.6 Research aim and objectives

The aim of this research is to quantify the spatial and temporal patterns in the movements of a ubiquitous lowland river fish and explore their ecological implications, in a period covering three annual reproductive seasons and in a heterogenous river system of high lateral and longitudinal connectivity. Using common bream as the study species and the River Bure system, in Norfolk, eastern England, as the study area, the research objectives (O) are to:

O1. Assess the limitations of applying acoustic telemetry to studying the movement behaviour of fishes in a lowland wetland system, and identify the best practice measures that help overcome these;

O2. Integrate ecological stable isotope analyses with acoustic telemetry to identify how these methods can be used in a complementary manner to predict long-term movements of lowland fish;

O3. Determine the movement patterns of common bream over successive years to test the repeatability of individual movements across time and space, including during annual reproductive seasons; and

O4. Identify whether high lateral and longitudinal river connectivity results in high levels of mixing across individuals within wetland systems at key periods of the year and in the lifecycle of the fish.

These research objectives are met in the data chapters as follows:

Chapter 2: Testing the detection range and/or detection efficiency of acoustic receivers and assessing the influence of environmental variables on their performance (O1).

Chapter 3: Investigating the post-acoustic tagging survival rates of lowland river fishes in the wild (O1).

Chapter 4: Applying dual-isotope isoscapes to predict the movements of riverine fishes and comparing predictions with movement data from acoustic telemetry (O2).

Chapter 5: Examining the diversity of bream migration behaviour in a highly-connected, lowland system (O3).

Chapter 6: Quantifying the temporal and spatial consistency of bream migratory phenotypes and determining their social preferences and extent of population mixing during their annual spawning periods (O4).

2 High temporal and spatial variability in the detection efficiency of acoustic telemetry receivers in a connected wetland system

2.1 Abstract

Acoustic telemetry is an important tool for assessing the behavioural ecology of aquatic animals, but the performance of receivers can vary spatially and temporally according to changes in environmental gradients. Studies testing detection efficiency and/ or detection range are therefore important for data interpretation, although the most thorough range-testing approaches are often costly or impractical, such as the use of fixed sentinel tags. Here, stationary tag data (from study animals that had either died or expelled their tags) provided a substitute for the long-term monitoring of receiver performance in a wetland environment and was complemented by periodic boat-based range testing, with testing of the effects of environmental variables (water temperature, conductivity, transparency, precipitation, wind speed, acoustic noise) on detection efficiency (DE) and detection range (DR). Stationary tag DE was highly variable temporally, with the most influential factors being water temperature and precipitation. Transparency was a strong predictor of DR and was dependent on chlorophyll concentration (a surrogate measure of algal density). These results highlight the value of stationary tag data in assessments of acoustic receiver performance. The high seasonal variability in DE and DR emphasises the need for long-term receiver monitoring to enable robust conclusions to be drawn from telemetry data.

2.2 Introduction

The application of acoustic telemetry to examining the space-use and behaviour of aquatic animals has grown exponentially in recent decades (Hussey et al. 2015). It has benefitted from rapid technological development (e.g. Klinard et al. 2019b, Reubens et al. 2019), resulting in a wealth of data to support species and habitat management (Brooks et al. 2019) in both the marine and freshwater environments (e.g. Davies et al. 2020).

Passive acoustic telemetry functions by transmission of coded ultrasonic signals between tags (transmitters implanted in/ attached to moving organisms) and submerged hydrophones coupled with receivers ('receivers' hereafter), which are usually positioned at fixed locations. When a tag is within detection range of a receiver, its unique identity is recorded, along with a date-time stamp. Data can be collected continuously for multiple individuals across broad spatial scales, providing distinct advantages over more traditional methods of active animal tracking (Kessel et al. 2014b). Furthermore, technological advances are reflected in extended battery lives of tags. In response, the duration of studies has expanded from hours to multiple years (Hussey et al. 2015). Consequently, aquatic acoustic tracking is increasingly conducted across a broad range of environments, from the Amazon (Hahn et al. 2019) to the Arctic (Kessel et al. 2016), and under environmental conditions that can fluctuate considerably over time. However, assessments of how the performance of receivers varies over time and space have been less frequent (Kessel et al. 2014b), risking the misinterpretation of animal behaviour if the frequency of acoustic detections do not directly represent the space-use and activity of tagged animals (Payne et al. 2010).

The successful transmission of an acoustic signal over a specific distance depends on several factors, including the intensity of the signal at the point of generation (i.e. tag power output); the amount of signal loss due to spreading, refraction, reflection and absorption by the water and other objects; and the extent of interference from background noise (Medwin and Clay 1998). These factors are controlled by many variables, some of which may be constant through time and so can be accounted for at the study onset, such as habitat type (e.g. depth, substrate; Selby et al. 2016), transmitter type (How and de Lestang 2012), transmitter location (e.g. internal or external attachment; Dance et al. 2016) and receiver mooring design (Clements et al. 2005, Huveneers et al. 2016). Other variables affecting the ability of receivers to detect transmitters may fluctuate substantially over a study period, such as tag orientation (Ammann 2020) the physical or chemical properties of water (e.g. temperature, salinity, turbidity; Huveneers et al. 2016), water movement (e.g. waves, tides, river flows; How and de Lestang 2012, Mathies et al. 2014), meteorological conditions (e.g. wind, rain; Gjelland and Hedger 2013), biofouling (Heupel et al.

2008) and/ or ambient, anthropogenic and biotic noise (Payne et al. 2010, Reubens et al. 2019). In addition, signal collisions can occur when the transmissions of multiple tags interfere with each other (Simpfendorfer et al. 2008, Pincock 2012). While this is minimised by tags with random transmission intervals, it has implications if study species form large aggregations within range of receivers.

As a result of these inconsistencies, analyses of acoustic telemetry data require an understanding of the variability in the probability of detection over space and time if researchers are to examine rates of movement, space-use and/ or activity, as opposed to simply recording the movement trajectories of animals. Detection efficiency (DE), defined as the number of detections in a set period as a proportion of the total number possible (Brownscombe et al. 2020), typically shows a logistic relationship of decay with increasing distance from an acoustic receiver (Kessel et al. 2014b). Assessment of DE can be completed in a number of ways, the most thorough being the use of fixed sentinel tags at regular distance intervals from focal receivers (Kessel et al. 2014b, Selby et al. 2016, Brownscombe et al. 2020). However, comparatively few studies have adopted this method in riverine or wetland environments (but see Whitty et al. 2009, Béguer-Pon et al. 2015), perhaps because feasibility is limited by factors that prevent safe deployment, such as high flow variability and/ or high anthropogenic disturbance in navigable waterways.

In highly connected wetlands, where the habitats used by fishes can include a range of lentic and lotic areas, the prevailing environmental conditions can vary spatially and temporally, potentially impacting both DE and detection range (DR). This is particularly pertinent to the Norfolk Broads, eastern England, where the landscape includes nutrient rich, shallow lakes connected to lowland rivers used for navigation. Using this area as the study system, the aim was to assess spatial and temporal variability in the detection range and efficiency of acoustic receivers. High levels of boat traffic in this shallow environment prevented the use of sentinel transmitters moored at fixed distances from receivers. However, during the study period, it became apparent that stationary transmitters were present in the vicinity of some receivers, having either been expelled by tagged fish or the tagged fish had died there. These transmitters enabled the continuous monitoring of receiver DE for up to

16 months. With this complemented by periodic boat-based range testing, the study objective was thus to quantify both acoustic receiver DE and DR, and test changes in these in relation to temporally variable environmental conditions.

2.3 Materials and Methods

2.3.1 Study system

The focus of the study was the River Bure, which forms part of the Broads National Park, a protected wetland characterised by many small shallow lakes (medieval peat diggings termed 'Broads'; Figure 2.1). The system is tidal and experiences major saline incursions during tidal surges and/ or low river flows, generally in winter, with the upstream limit of saline intrusion believed to be at Horning (Figure 2.1; Clarke 1990). The Bure flows south-east into the North Sea, with a mean discharge of 6 m^3s^{-1} (Moss 1977). Its channel widths in the study area are 25-30 m wide, with depths to 3 m, and a substrate predominantly consisting of silt and peat.

A fixed array of 44 acoustic receivers (Vemco, VR2W) was deployed in the river and connected wetlands in October 2017 and January 2018 to track the movements of native fish species. Measures of DE or DR were estimated for nine receivers that covered both lentic and lotic habitats (Table 2.1; Figure 2.1). Data were downloaded quarterly, when the hydrophones were also cleaned of biofouling. Receivers were attached to permanent underwater structures, moored on wooden posts or suspended from floating objects (Table 2.1), and were continuously operational until the study end in November 2019. All receivers were placed at approximately mid-water depth (1-1.5 m) and were generally positioned in channel/ lake margins.

2.3.2 Stationary tags

Common bream *Abramis brama* (L.) were sampled from the River Bure by rod and line angling during November 2017 and April 2018. Under anaesthesia (Tricaine methanesulfonate, MS-222), fish were surgically implanted with an acoustic transmitter ('tag' hereafter) (V13: 69 kHz; length 36 mm × diameter 13 mm, 6.0 g

mass in water; random transmission interval around 90 s; estimated battery life 1200 days) and released following their return to normal behaviour. All regulated procedures were performed under the UK Home Office project licence 70/8063 and after ethical review. Between 18 January 2018 and 15 May 2019, eight tags became stationary within range of an acoustic receiver (Figure 2.1), either due to fish death or tag expulsion. Three of these tags were located using manual acoustic tracking (Vemco, VR100) and their distance to the nearest acoustic receiver was estimated (± 25 m; Table 2.1). Other tags could not be located due to constraints imposed by resource restrictions. Detection data from all stationary tags were collected until 5 November 2019, except for one tag whose data were collected from 5 April 2018 to 1 August 2018, after which it was no longer in range of a receiver due to it being redeployed in a different location (Receiver #4; Table 2.1; Figure 2.1). Another receiver (Receiver #6) was moved by approximately 100 m during the study period, while the nearby stationary tag remained in range; for this tag, the pre- and post-relocation data were separated (Figure 2.2).

2.3.3 Detection range testing

A total of 14 range tests were conducted for two receivers situated in Wroxham Broad (WB; N = 8) and South Walsham Broad (SWB; N = 6) between January and November 2019 (Figure 2.1). These locations offered sufficient space for range testing, while representative of distinct environmental conditions. WB is situated upstream of the saline limit at Horning and has a relatively high exchange of water with the River Bure, while SWB is situated further downstream, below the limit of saline incursion, but is much less strongly influenced by main river flows. Due to its location, SWB is at risk of high saline events (especially in winter) and typically displays higher residual conductivity (as a measure of salinity) than WB. In addition, the release of phosphorus from the sediment in SWB results in dense blooms of phytoplankton during warmer months (Moss and Balls 1989). In each location, DR was estimated by lowering a range testing tag (V13; 69 kHz; fixed 10 second transmission interval) from a stationary boat to 1 m below the water surface at distance intervals of approximately 50 m from the receiver. The tag was held underwater for one minute, and DR was recorded as the maximum distance over

which the tag remained detectable. Exact distances were verified using GPS positions taken during range testing.

2.3.4 Environmental data

Water temperature (± 0.5 ˚C) in the River Bure was recorded at 15-minute intervals throughout the study period by a data logger (HOBO® Pendant; model MX2202, Onset Computer Corporation; Figure 2.1). Half-hourly records of average wind speed (ms^{-1}) at Norwich airport (10 km from study site), plus six-hourly records of precipitation (cm) at the MET office station at Weybourne (33 km from study site), were obtained from an online meteorological archive (Raspisaniye Pogodi Ltd 2020). During range testing in WB and SWB, point measurements of water temperature (± 0.2 ˚C) and conductivity (± 0.005 $mS \cdot cm^{-1}$) were taken using a YSI meter (Pro Plus), with water transparency (± 0.1 m) measured using a Secchi disk. Further data on water transparency and chlorophyll (*a* and *b*) concentration, measured at monthly intervals between November 2017 and February 2020, were sourced for six locations across the study site (Figure 2.1; Environment Agency 2020b).

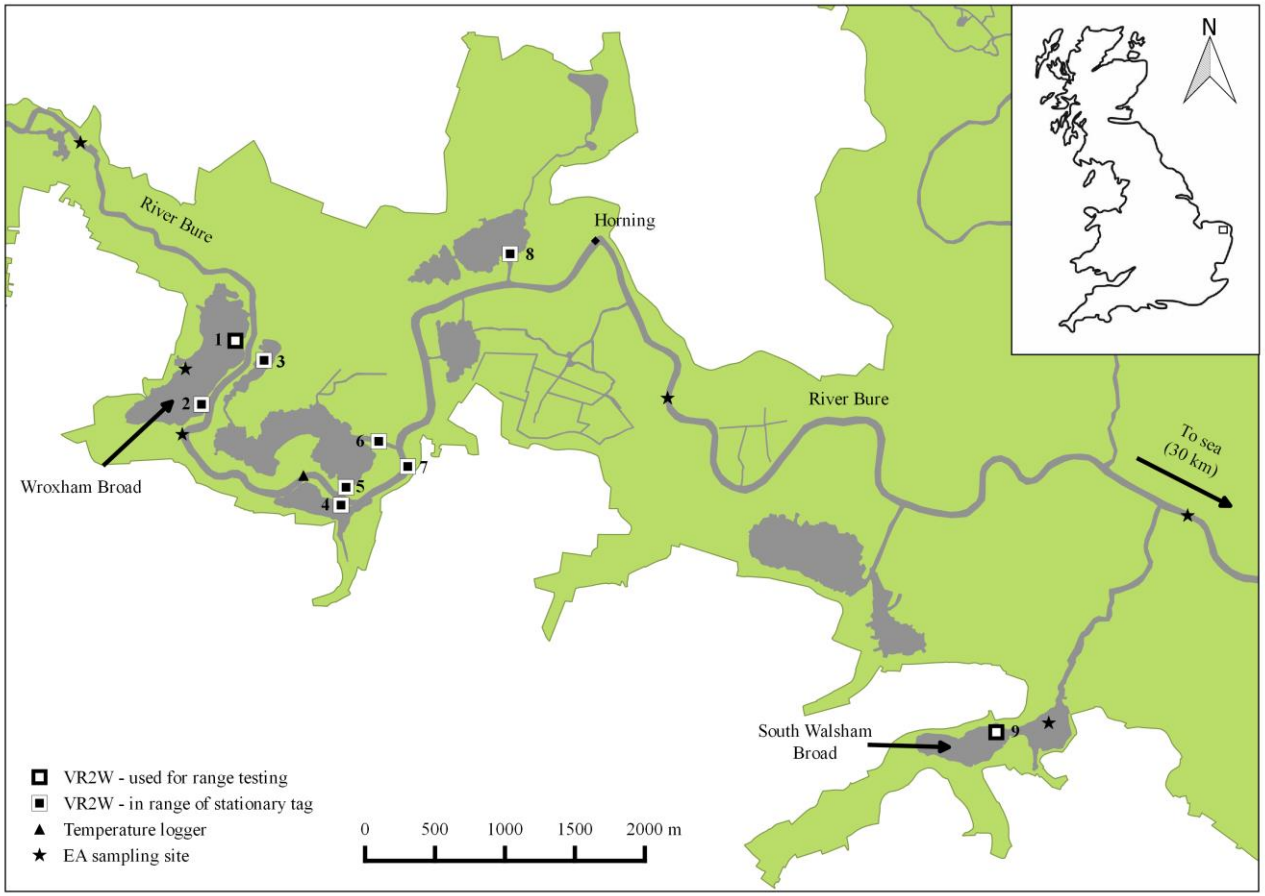

Figure 2.1: Map of the River Bure study system showing locations of the acoustic receivers used in range testing, plus those in range of stationary tags which were used to measure detection efficiency. Receivers are numbered according to Table 2.1. The location of the temperature logger and water sampling sites (Environment Agency 2020b) are also pictured. The Broads National Park area is shaded green.

Table 2.1: Details of acoustic receivers used in the study, including their application to measurements of either detection efficiency (DE) or detection range (DR). Receiver #6 was moved during data collection, so pre- and post-redeployment data were separated (Figure 2.2), resulting in two distance values.

Receiver #	Receiver mooring design	Habitat	Measure of receiver performance	Distance to stationary tag (m)
1	Attached to permanent wooden structure	Lentic; flowing	DR	NA
2	Moored on wooden post	Lentic; flowing	DE	Unknown
3	Suspended from pontoon	Lentic	DE	250
4	Moored on wooden post	Lentic; flowing	DE	100
5	Moored on wooden post	Lentic	DE	Unknown
6	Moored on wooden post	Lentic	DE	50; 150
7	Attached to permanent wooden structure	Lotic	DE	Unknown
8	Moored on wooden post	Lentic	DE	Unknown
9	Moored on wooden post	Lentic	DR	NA

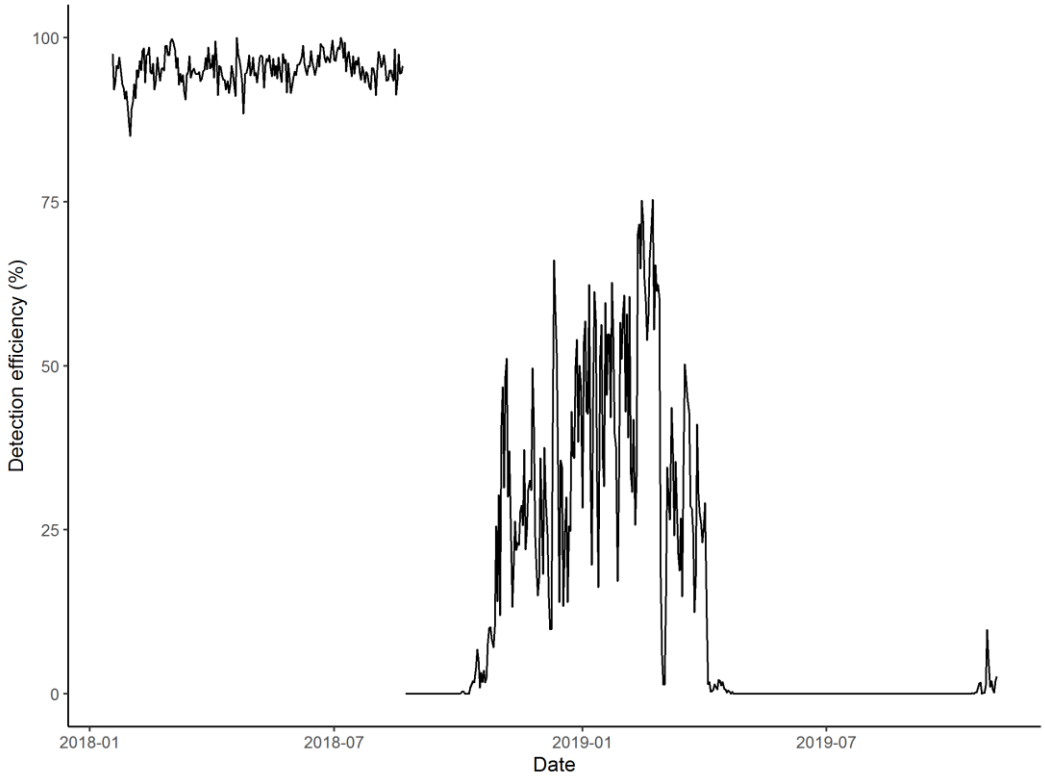

Figure 2.2: Daily detection efficiency of one stationary tag in range of an acoustic receiver. Separate lines represent data collected pre- and post-receiver redeployment on 22 August 2018. The transmitter was originally located to within 50 m of the receiver, but following receiver redeployment this distance increased to approximately 150 m.

2.3.5 Statistical analysis

First, the stationary tag data were tested in generalised linear mixed models (GLMM) to estimate the probability of detection as a function of mean daily water temperature, mean daily wind speed, total daily precipitation and the daily noise quotient. The noise quotient was calculated from summary data stored by the receivers (Simpfendorfer et al. 2008) and provided a measure of acoustic noise in the environment, with negative values indicating tag collisions and positive values indicating ambient/ anthropogenic/ biotic noise. The GLMM response variable was the daily number of recorded detections, as a proportion of the maximum number possible given the transmission interval. This required a binomial family structure and logit link function, with a random effect of tag ID accounting for variation in tag/ receiver habitat and distance from the receiver. Covariates were initially parameterised separately in univariate models, then combinations of those resulting in a reduction in Akaike's information criterion (AIC) values were compared in multivariate models. Model comparison followed the minimisation of AIC, with those exhibiting $\Delta AIC < 2$ awarded strong support alongside the best model, providing they were not more complex versions of nested models with lower AIC (Richards et al. 2011).

Next, the range testing data were tested in linear mixed models (LMM) to examine the effect of water temperature, conductivity, wind speed and transparency on the maximum DR of acoustic receivers, with receiver location (WB; SWB) included as a random effect. Seasonal fluctuations meant that temperature and transparency were correlated (WB: $r = -0.84$, $p = 0.009$; SWB: $r = -0.89$, $p = 0.016$), as well as temperature and conductivity at WB ($r = -0.86$, $p = 0.006$), and so these covariates were not modelled together. Model selection followed the minimisation of AIC, as above. Finally, the relationship between water transparency and chlorophyll concentration was explored using the water quality data in an LMM. Data were log-log transformed (Carlson 1977), with sample site representing a random effect. All analyses were conducted in R 3.6.2 (R Core Team 2019) using the package *lme4* (Bates et al. 2015).

2.4 Results

2.4.1 Detection efficiency

The daily detection efficiency (DE) of stationary tags was highly variable, both spatially and temporally (Figures 2.2, 2.3). All covariates in the univariate models, except wind speed, resulted in reduced AIC. Mean daily water temperature and total daily precipitation were retained in the best-fitting GLMM predicting DE, with both variables having a negative effect on the probability of detection (Table 2.2a; Figure 2.3). Water temperature was a particularly strong predictor of DE, with AIC increasing substantially when it was removed from the model (ΔAIC = 230; Appendix 1, Table A1.1). While the noise quotient varied from -114,660 to 391, with 87 % of values below zero, suggesting a high incidence of tag collisions, noise did not contribute to the best model predicting DE. No other combinations of variables were awarded strong support under the selection criteria (Appendix 1, Table A1.1). The estimated between-tag standard deviation was considerably larger than the magnitude of the fixed effects (Table 2.2a), indicating significant spatial variation in DE due to habitat and/ or distance from the receiver (Figure 2.3).

2.4.2 Detection range

Boat-based detection range testing was conducted over varying environmental conditions at both sites, with water temperature ranging from 2.9 to 23.1 °C, transparency from 0.3 to 2.0 m, and wind speed from 5 to 14 m s^{-1}. Conductivity at Wroxham Broad (WB) was stable (mean ± SD: 0.80 ± 0.03 mS·cm^{-1}), but at South Walsham Broad (SWB) varied from 0.83 to 5.69 mS·cm^{-1} (1.96 ± 1.88 mS·cm^{-1}). All covariates improved LMM fit relative to the null model, but the best model predicting DR retained transparency and wind speed (Table 2.2b), with no other combinations of covariates receiving strong support under the selection criteria (Appendix 1, Table A1.2). Notably, the removal of transparency resulted in a model with a relatively high ΔAIC value (19.3), indicating its high explanatory power (Figure 2.4; Appendix 1, Table A1.2). While wind speed was also included in the best model, uncertainty in the magnitude of its effect was high and overlapped zero

(Table 2.2b). Variation in DR according to the random effect of receiver location was low relative to the magnitude of the effect of transparency, but high relative to the effect of wind speed (Table 2.2b). In addition, chlorophyll concentration was a strong predictor of water transparency across the study system (Table 2.2c; Figure 2.5), reducing AIC by 92.2 relative to the null model.

Table 2.2: Coefficient estimates for the fixed (β ± SE) and random effects (SD) in the best fitting (a) GLMM predicting daily detection efficiency of stationary tags, (b) LMM predicting acoustic detection range of receivers and (c) LMM predicting water transparency.

Parameter	Fixed	Random
(a)		
(Intercept)	1.53 ± 1.16	-
Temperature	-0.21 ± 0.02	-
Precipitation	-0.08 ± 0.03	-
Tag ID	-	3.42
(b)		
(Intercept)	-51.18 ± 217.77	-
Transparency	437.85 ± 113.89	-
Wind speed	-7.23 ± 16.63	-
Receiver location	-	142.50
(c)		
(Intercept)	0.39 ± 0.04	-
Log(chlorophyll)	-0.32 ± 0.03	-
Sample site	-	0.07

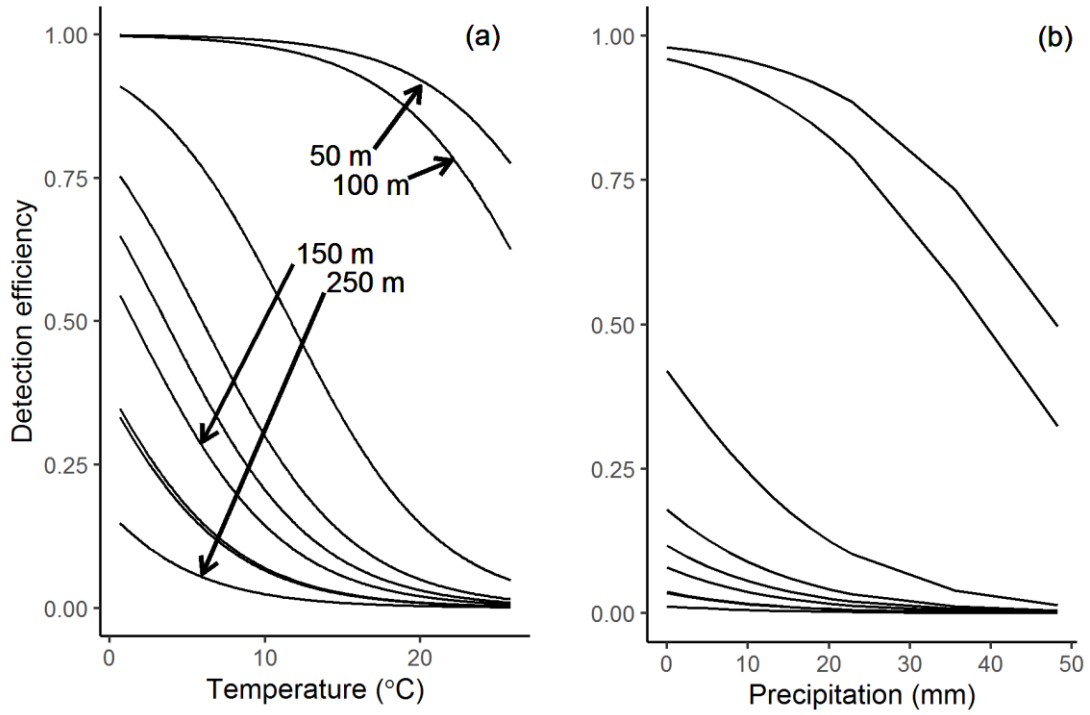

Figure 2.3: The effects of (a) mean daily temperature and (b) total daily precipitation on the detection efficiency of stationary tags according to the best-fitting GLMM model. Lines represent separate transmitter data included as a random effect. Labels in panel (a) signify the distance between certain transmitters and their nearest acoustic receiver.

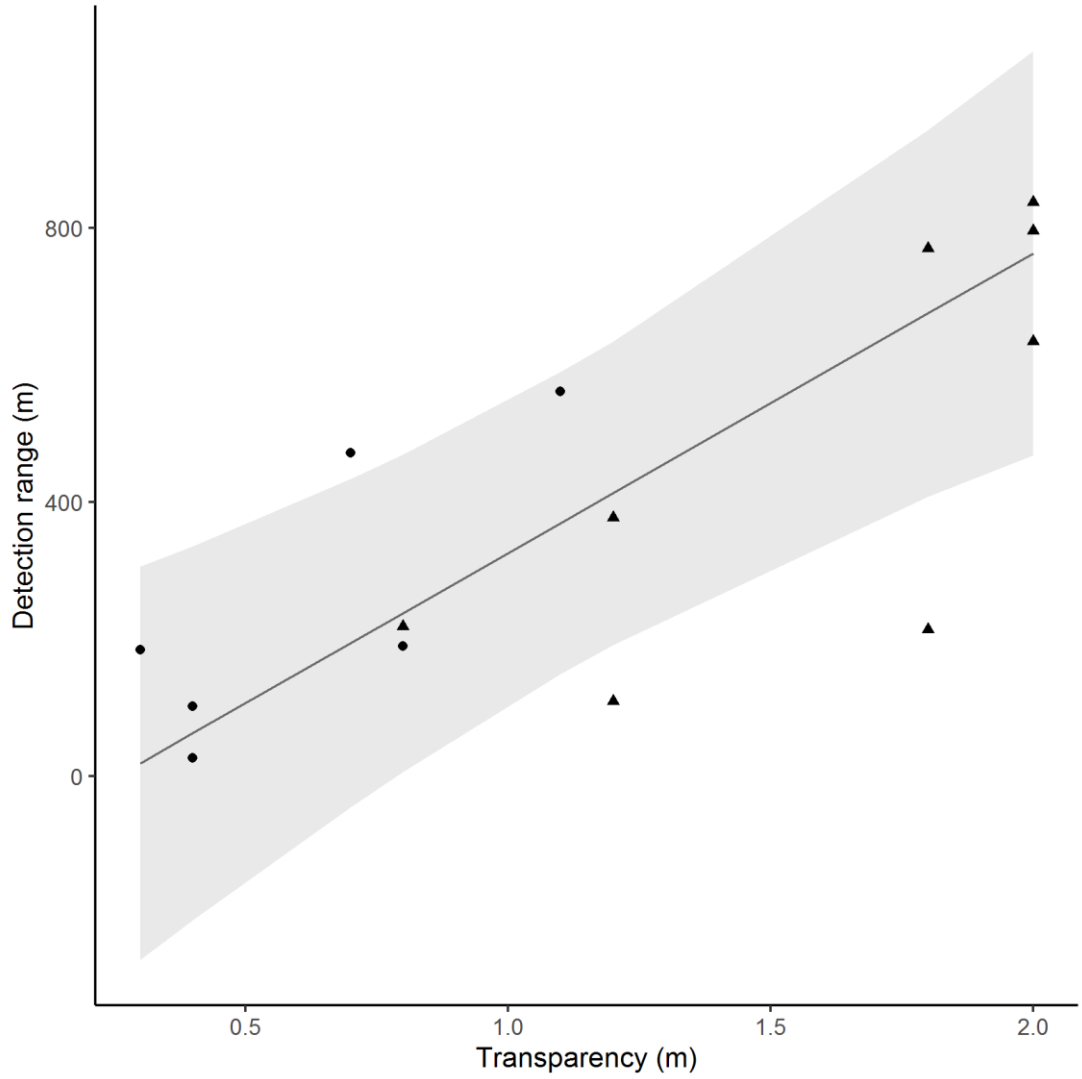

Figure 2.4: Effect of water transparency (as Secchi disk depth) on the maximum acoustic detection range measured periodically in Wroxham Broad (triangles) and South Walsham Broad (circles). The solid line and greyed area represent predictions and 95 % confidence intervals according to the best-fitting LMM.

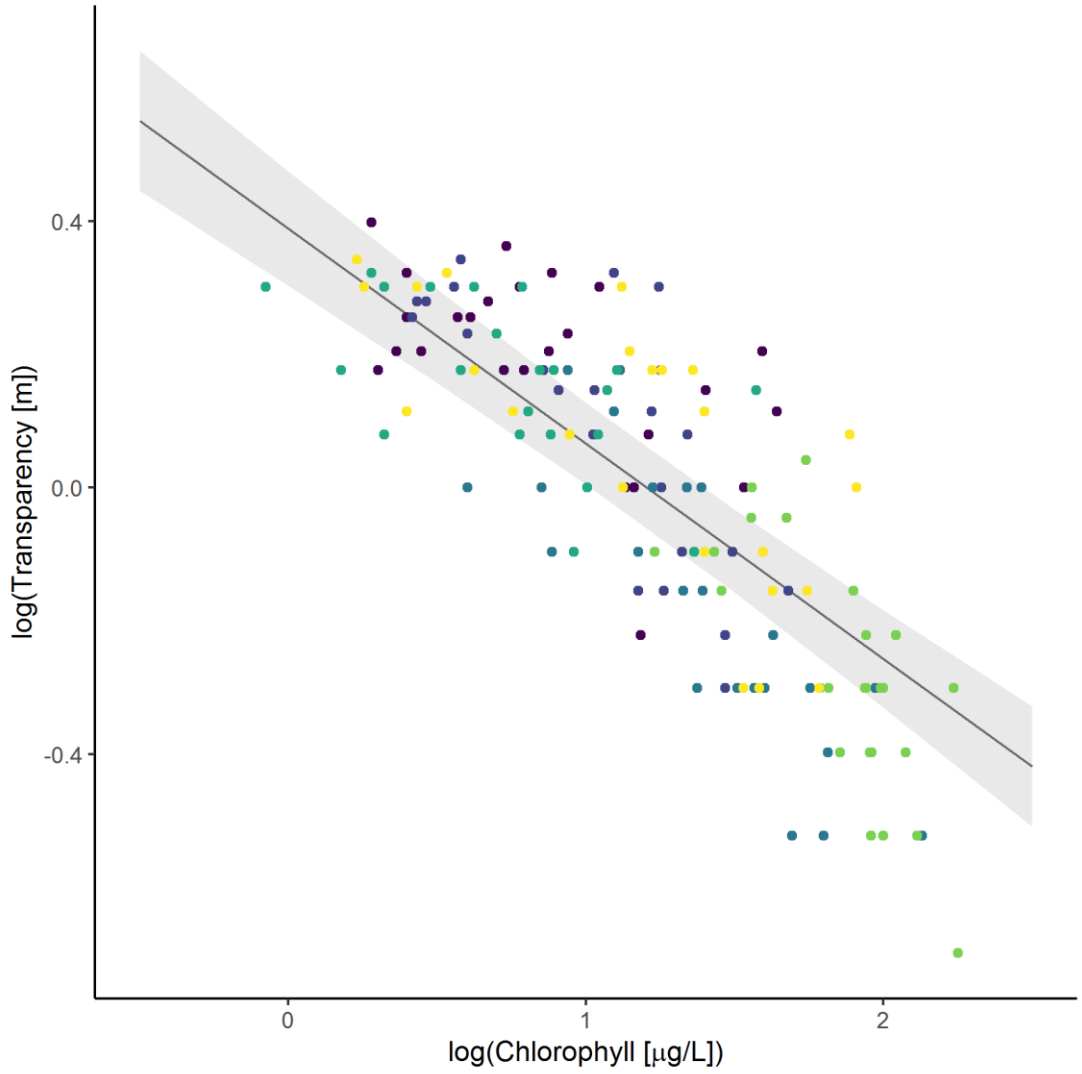

Figure 2.5: Effect of chlorophyll concentration on the transparency of water samples collected across the study site (Environment Agency 2020b). Sample sites are signified by point colour. The solid line and greyed area represent predictions and 95 % confidence intervals according to the best-fitting LMM.

2.5 Discussion

Awareness of issues surrounding the performance of receivers for acoustic telemetry has grown in recent years, with studies having increasingly investigated variability across biotic and abiotic gradients (Kessel et al. 2014b, Huveneers et al. 2016). Here, stationary transmitters in the environment enabled the measurement of the long-term DE of receivers in an environment where the deployment of sentinel tags was not feasible. The results revealed high spatial and temporal variability in receiver performance; daily detection efficiency decreased with elevated water temperature and precipitation, and variability between tags indicated a dependence on transmission distance and habitat typology. Complementary boat-based range testing revealed water transparency to be a strong predictor of maximum detection range.

Temperature affects the propagation of sound in water through its impact on water density (Medwin and Clay 1998). How and de Lestang (2012) also reported a reduction in DE with increased temperature, although other studies have reported no significant correlation (Heupel et al. 2008, Gjelland and Hedger 2013). While thermal stratification of water is key to explaining reduced DE in some systems (e.g. Huveneers et al. 2016, Klinard et al. 2019a), it is unlikely to apply to the River Bure as depths do not exceed 4 to 5 m, and even less probable in broads with mean water depths of 1.5 – 2 m. Alternatively, water temperature may be associated with other factors affecting DE in the study system, such as seasonal anthropogenic noise (i.e. boat traffic related to tourism, Moss 1977), algal blooms (Moss and Balls 1989) and/ or macrophyte growth (Weinz 2020). Indeed, periodic range testing revealed transparency (or turbidity) was a better predictor of maximum DR than temperature. Furthermore, the results revealed a clear association between transparency and chlorophyll concentration, which is an indicator of the density of algal blooms (Moss and Balls 1989). This finding is consistent with a number of other studies suggesting phytoplankton impacts acoustic receiver performance (Shroyer and Logsdon 2009, Gjelland and Hedger 2013). Consequently, water temperature may be both directly and indirectly linked to the temporal fluctuations in DE observed here.

The influence of precipitation and wind is expected to be more prominent in shallow water than at depth due to the entrainment of air bubbles that enhances sound absorption and scattering (Gjelland and Hedger 2013). While evidence here suggested rain reduced DE, wind speed could not predict DE and its effect on DR was uncertain. This is perhaps due to the relatively sheltered nature of the study system compared to large lacustrine, estuarine or marine sites that feature in other range-testing studies (e.g. Gjelland and Hedger 2013, Huveneers et al. 2016, Reubens et al. 2019). Conductivity was not a strong predictor of DR, but Heupel et al. (2006) reported reduced DR in freshwater versus estuarine sites, with Simpfendorfer et al. (2008) suggesting that the stratification of water in estuaries can lead to greater acoustic interference. This emphasises the need for more detailed investigation into the effect of salinity gradients on acoustic receiver ranges.

The study system was characterised by a predominantly silt sediment, upon or within which the stationary tags would have settled. Acoustic receivers can exhibit higher detection range in environments with more homogenous substrates (Selby et al. 2016, Brownscombe et al. 2020), although the detection of tags on or embedded in soft sediment is likely to be less efficient than tags suspended in the water column (Heupel et al. 2006). Therefore, some variation from the results here would be expected if the experiment were to be repeated with fixed sentinel tags. Nevertheless, evidence suggests that traditional range testing methods can considerably overestimate the detection probability of tagged animals *in situ* (Dance et al. 2016), and thus these estimates of DE may be more representative of the detection of benthic foraging fish species, such as common bream.

Few studies have examined long-term variability in acoustic receiver DE and/ or DR (for 12+ months; Kessel et al. 2014b, Huveneers et al. 2016). The patterns detected here highlight the importance of capturing the effects of natural seasonally fluctuating conditions. Adopting a fixed sentinel tag approach can be costly or inappropriate, especially if receivers are sparsely dispersed throughout a heterogeneous environment (Kessel et al. 2014b, Brownscombe et al. 2020). This study demonstrates the utility of exploiting data from stationary tags that could otherwise be overlooked. The unpredictable nature of animal death and/ or tag

expulsion, along with a lack of knowledge regarding the precise locations of tags, presents some obvious limitations of incorporating this technique into study designs. However, the results indicate that stationary tag data, if available, can provide equally valuable information on acoustic receiver performance, when compared to active range testing.

3 Predicting the factors influencing the inter- and intra-specific survival rates of riverine fishes implanted with acoustic transmitters

3.1 Abstract

Biotelemetry is a central tool for fisheries management, with the implantation of transmitters into animals requiring refined surgical techniques that maximise retention rates and fish welfare. Even following successful surgery, long-term post-release survival rates can vary considerably, although knowledge is limited for many species. The aim here was to investigate the post-tagging survival rates in the wild of two lowland river fish species, common bream *Abramis brama* and northern pike *Esox lucius*, following their intra-peritoneal double-tagging with acoustic transmitters and passive integrated transponder (PIT) tags. Survival over a two-year period was assessed using acoustic transmitter data in Cox proportional hazards models. Post-tagging survival rates were lowest in the reproductive periods of both species, but in bream, fish tagged just prior to spawning actually had the highest subsequent survival rates. Pike survival was influenced by sex, with males generally surviving longer than females. PIT tag detections at fixed stations identified bream that remained active, despite loss of an acoustic transmitter signal. In these instances, loss of the acoustic signal occurred up to 215 days post-tagging and only during late spring or summer, indicating a role of elevated temperature, while PIT detections occurred between 18 and 359 days after the final acoustic detections. Biotelemetry studies must thus always consider the date of tagging as a fundamental component of study designs in order to avoid tagged fish having premature end points within telemetry studies.

3.2 Introduction

Biotelemetry has developed into a central tool for fisheries management, providing valuable information on population dynamics, fish behaviours and movements, habitat connectivity, and even inter-specific relationships (e.g. Hussey et al. 2015, Halfyard et al. 2017). The technology of tracking devices has advanced considerably in recent decades, from simple, passive, externally-attached markers to active,

internally-implanted transmitters, or 'tags', that can broadcast a multitude of information over large distances (Lucas and Baras 2001, Hussey et al. 2015). As a result, the interpretation of telemetry data has become increasingly complex, requiring consideration of several limitations, such as signal interference (Simpfendorfer et al. 2008), detection range/ efficiency (Chapter 2; Huveneers et al. 2016) and the effects of tagging on study animals (Bridger and Booth 2003).

The implantation of transmitters into fish (and other animals) requires refined surgical techniques completed by experienced practitioners, in order to minimise the adverse effects on the welfare of the animal (Bolland et al. 2019, Skov et al. 2020). This should ensure that the survival of the tagged animal is not compromised and that it also returns to normal behaviour relatively quickly (Moore et al. 1990, Cooke et al. 2011). More fundamentally, the tagged individuals should be representative of the wider, untagged population (Bridger and Booth 2003), yet many studies evidence inter- and intra-specific variation in post-tagging success. For example, intracoelomic tag implantation maximises survival and recovery of fusiform fishes when compared to external tag attachment (Jepsen et al. 2002, Bégout Anras et al. 2003, Cooke et al. 2011), but can result in poorer survival and altered behaviour in flatfishes such as the European flounder (*Platichthys flesus,* L.) (Neves et al. 2018). Within species, tagging success may be dependent on body size relative to tag size (Welch et al. 2007). It can also vary by sex, with some studies reporting lower survival and tag retention in females (Jepsen et al. 2002, Šmejkal et al. 2019). Furthermore, environmental factors can influence fish responses to tagging, particularly water temperature, with elevated temperatures tending to reduce survival and welfare (Walsh et al. 2000, Yasuda et al. 2015).

Ultimately, research objectives, study design and data interpretation are driven by knowledge of the impacts of tagging on fish survival and behaviour (Donaldson et al. 2014). This includes the planning of sampling and release protocols, tagging procedures and timeframes of subsequent telemetry (Bolland et al. 2019). However, of studies that apply acoustic telemetry to aquatic ecology/ behavioural research, around 50 % fail to account for or acknowledge mortality of the study species (Klinard and Matley 2020), and a standardised method for identifying the fates of

tagged fish (e.g. survival, natural mortality, fishing mortality) has only recently been developed (Villegas-Ríos et al. 2020). Consequently, as the diversity of tracking technologies and tracked fish species expands, including a wider range of fish sizes and morphologies, such as Anguillids and flatfish (Thorstad et al. 2013, Neves et al. 2018), knowledge gaps surrounding the effects of telemetry are potentially widening. This can be especially problematic for researchers studying species where information is more limited, as it constrains their ability to optimise tagging procedures in relation to maximising fish welfare and survival or draw robust conclusions from the resulting data.

The aim of this study was thus to investigate the survival rates of two lowland river fish species following their intra-peritoneal double-tagging with acoustic transmitters and passive integrated transponder (PIT) tags, and their subsequent release back into the wild. The two species were common bream (*Abramis brama, L.*; 'bream' hereafter), a cyprinid that often dominates the biomass of lowland river fish assemblages in northwest Europe (Lyons and Lucas 2002), and northern pike (*Esox lucius, L.*; 'pike' hereafter), an apex predator (Beaudoin et al. 1999). Survival within the study was assessed using data from the acoustic transmitters, with survival over a two-year post-tagging period requiring the fish to remain alive, stay within the study area and continue to transmit acoustic signals via their tags. As a result of the multi-method, double-tagging approach, PIT tag data were then used to categorise fish that had not 'survived' into those that had actually died and those that remained active, but whose acoustic signals had been lost. The study objectives were thus to: (1) assess the survival rates of the two fishes in relation to their individual characteristics, and the timing and location of tagging; and (2) for those fish that did not survive within the study, assess their fate (death, leaving the study area, or loss of the acoustic tag signal, such as through tag failure or tag expulsion).

3.3 Materials and Methods

3.3.1 Study system and telemetry equipment

The study system was the River Bure in eastern England, along with its tributaries the Rivers Ant and Thurne, plus associated small shallow lakes (medieval peat diggings termed 'Broads') and dykes, which form the northern area of the Broads National Park (Figure 3.1). The Bure is 87 km in length, flows south-east towards Breydon Water estuary at Great Yarmouth, and has a mean discharge of 6 $m^3 \cdot s^{-1}$ into the North Sea (Moss 1977). By contrast, the Ant is 27 km in length and the Thurne is just 11 km in length. Conductivity (as a measure of salinity) can fluctuate between 1,000 and 50,000 $\mu S \cdot cm^{-1}$ at Acle (Figure 3.1), with major saline incursions often occurring during spring tides in winter and early spring (Clarke, 1990). Channel widths towards the upper limits of the study area were approximately 25 m wide with depths to 1.5 m, while in the lower reaches they increased to > 40 m, with depths of over 3 m. Across the study area, bream tend to spawn in late April and throughout May, and pike in late March to mid-April.

A fixed array of 43 acoustic receivers (Vemco, VR2W) was installed throughout the study system (Figure 3.1) in October 2017, prior to the first fish sampling and tagging event. A further 13 receivers were deployed in January 2018 (N = 1) and in March 2019 (N = 12) to expand the monitored area (Figure 3.1). Receiver coverage was optimised to monitor longitudinal riverine movements to at least 6 km resolution, as well as finer-scale lateral movements. Data were downloaded every three months onto a laptop, while battery replacements and receiver maintenance occurred annually. This enabled the tracking of fish implanted with acoustic transmitters until the study end in November 2019. Receivers were placed in the channel margins at approximately mid-water depth (1.0 - 1.5 m) to optimise detection efficiency. Range testing revealed some variability in detection distances that correlated to changes in environmental conditions (Chapter 2), but which rarely fell below channel width distance.

Acoustic telemetry was deemed inappropriate for tracking fish in the small marshland drainage channels of the study system, but utilising multi-method telemetry can be useful for monitoring fish movements at varying spatial scales (e.g. Tummers et al. 2016). Thus, six stream-width, swim-through half-duplex (HDX) RFID PIT antennae (15 – 30 m circumference), with remote, telemetric, web-based data logging systems (Wyre Micro Development, Bungay, Suffolk, UK), were constructed and installed in dykes in March 2018 (Figure 3.1). PIT tags were detected by WMD-HDX-DEC-MK5 readers that interrogated the loops continually and recorded tag presence 10 times per second. Data were transmitted to a cloud-based server via a multi-band roaming sim modem (WMD-MC-GPRS/GSM) and accessed remotely. Minimum horizontal detection range for 23 mm tags (see below) was measured at installation (approx. 40cm) and the tuning frequency of each loop was maintained using a digital dynamic antenna tuning unit (WMD-DDATU). The RFID PIT detector systems were powered by 2 x 12 V 120 A batteries (wired in parallel) which were charged via solar arrays and maintained by a configurable charge controller and power supply filter that limited noise (WMD-MSC-45; WMD-PS-F). Each PIT antenna was operational for between 37 and 68 % of the study period; periods of non-operation were at least partly due to inconsistent power supply (e.g. due to failure to keep solar panels clear of undergrowth or damage to equipment by boats), which were identified using half-hourly records of battery status and antenna frequency.

In addition, water temperature (± 0.5 °C) was recorded at hourly intervals by a data logger (HOBO® Pendant; model MX2202, Onset Computer Corporation; Figure 3.1).

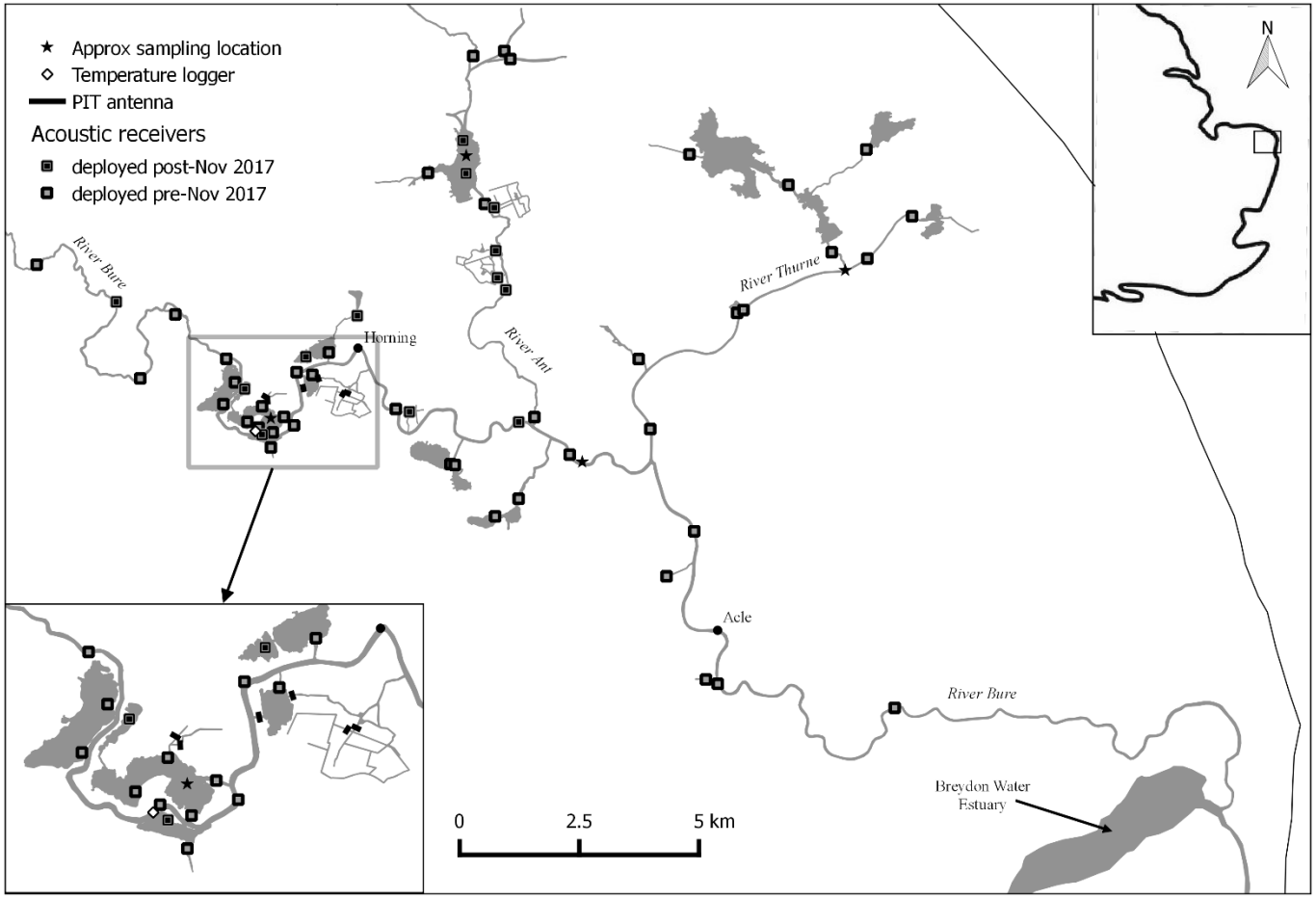

Figure 3.1: Map of the River Bure study system, eastern England, showing locations of sampling locations, acoustic receivers, PIT antennae and temperature logger. Channel width not to scale.

3.3.2 Fish sampling and tagging

The study area was divided into four sampling locations: Upper Bure, Lower Bure, River Ant and River Thurne. The upper limit of saline incursion on the River Bure (Horning, Figure 3.1; Clarke 1990) provided the boundary between the Upper Bure and the Lower Bure. Several fish sampling and tagging events occurred between November 2017 and September 2018, with details of their timing and location in Table 3.1. Water temperature during the November 2017 and January 2018 tagging events was 5.0 to 9.4 °C, while during the April 2018 and September 2018 events it was 15.0 to 17.8 °C. Fish were then tracked for up to two years to 5 November 2019. In all sampling, bream and pike were caught by rod and line angling, as sampling by methods such as electric fishing, seine netting and fyke netting were too inefficient in these large waterbodies (Radinger et al. 2019). Bream were captured using ledger rods and monofilament lines, with groundbait mixes in swim-feeders and worms or maggots presented on hooks close to the substrate. Pike were captured using specialist rods, braided fishing line (>40 lbs breaking strain) and wire traces to prevent the fish biting through the line, and used with either dead-bait (marine and freshwater fishes) or spinners, spoons and lures (hard and soft bodied artificial fishes). Each captured fish was measured (fork length; ± 1 mm; Table 3.1) and, where possible, sexed. Sex determination in both species involved inspecting the shape of the urogenital opening (e.g. Casselman 1974). For bream sampled during the spawning season (April 2018), other characteristics also informed sex determination, such as body shape, the presence of spawning tubercles on the head and the production of milt when lightly pressing the abdomen (when the fish were under general anaesthesia).

Each fish was surgically implanted with an internal acoustic transmitter (‘tag’) sourced from Vemco (V13: length 36 mm × diameter 13 mm, 6.0 g mass in water, N = 193; V9: length 27.5 mm × diameter 9 mm, 2.7 g mass in water, N = 9) or Thelma Biotel (ID-LP13: length 28 mm × diameter 13 mm, 5.5 g mass in water, N = 24). Acoustic tags operated at 69 kHz and were set to pulse randomly every 60 to 120 s, providing battery lives of between 29 and 46 months, depending on transmitter type. Random transmission intervals ensured adjacent signals did not continuously overlap

and cause interference. Noise quotients, calculated from summary data stored by the receivers (Simpfendorfer et al. 2008), revealed interference due to tag collisions at some receivers, but this was not a strong predictor of acoustic detection efficiency (Chapter 2). All fishes were additionally tagged with an internal passive integrated transponder (PIT) tag (Wyre Micro Developments: model WMD-HDX-GL-BAR , length 23.0 mm × diameter 3.35 mm, 0.6 g mass in air, 134.2 kHz), suited for use with fixed monitoring stations (Lucas and Baras 2000, Zydlewski et al. 2001). All regulated procedures were performed by the same surgeon whilst the fish were under general anaesthesia (Tricaine methanesulfonate, MS-222), and under the UK Home Office project licence 70/8063 and after ethical review. Iodine solution was used to disinfect surgical instruments and scales were removed from the incision site to aid scalpel and suture entry. Both acoustic and PIT tags were inserted ventrally and anterior to the pelvic fins, at the same incision site, with incisions then closed using a single suture and wound sealer. All fish were returned alive to the river following their postoperative recovery and return to normal body orientation and swimming behaviour.

Table 3.1: Details of common bream (a) and pike (b) tagging dates, fish lengths, acoustic tracking durations and proportion of days detected (P_d), grouped by sampling location. Length of fish and tracking duration are represented by the range of values, with mean ± 95% CI in parentheses, while P_d represents the mean ± 95% CI. 'N total' represents the sample size, while 'N lost to study' represents the number lost due to disappearance from the acoustic array or a signal becoming stationary. Numbers of fish detected on the PIT antennae are also presented.

Sampling location	Tagging date(s)	Length (mm)	Tracking duration (days)	Proportion of days detected	N total	N lost to study	N detected on PIT antennae
a) Bream							
Upper Bure	6 Nov 2017 – 8 Nov 2017	374 – 491 (435 ± 11)	0 – 725 (217 ± 76)	0.84 ± 0.04	26	23	2
Upper Bure	20 Apr 2018 – 23 Apr 2018	313 – 527 (413 ± 11)	18 – 562 (414 ± 54)	0.56 ± 0.07	62	22	14
Lower Bure	8 Nov 2017 – 9 Nov 2017	286 – 471 (362 ± 47)	25 – 524 (181 ± 120)	0.56 ± 0.18	8	8	0
Lower Bure	15 Sep 2018 – 18 Sep 2018	290 – 503 (389 ± 16)	2 – 414 (177 ± 44)	0.53 ± 0.07	43	34	0
Thurne	14 Jan 2018	341 – 471 (394 ± 15)	40 – 371 (132 ± 38)	0.44 ± 0.08	17	17	1
Ant	27 Jan 2018 – 29 Jan 2018	362 – 502 (406 ± 13)	28 – 645 (286 ± 92)	0.22 ± 0.07	25	20	1

(continued overleaf)

(Table 3.1 continued)

Sampling location	Tagging date(s)	Length (mm)	Tracking duration (days)	Proportion of days detected	N total	N lost to study	N detected on PIT antennae
b) Pike							
Upper Bure	6 Nov 2017 – 8 Nov 2017	583 – 1014 (780 ± 64)	4 – 727 (477 ± 144)	0.54 ± 0.16	15	7	0
Lower Bure	8 Nov 2017	776	124	0.81	1	1	0
Lower Bure	16 Jan 2018 & 28 Jan 2018	682 – 859 (774 ± 100)	422 – 644 (563 ± 139)	0.69 ± 0.16	3	1	0
Lower Bure	16 Sep 2018	590	413	0.20	1	0	0
Thurne	13 Jan 2018 – 15 Jan 2018	590 – 1143 (766 ± 69)	13 – 659 (434 ± 143)	0.37 ± 0.09	14	6	0
Ant	27 Jan 2018 – 28 Jan 2018	570 – 935 (758 ± 76)	5 – 645 (373 ± 143)	0.26 ± 0.12	11	7	0

3.3.3 Survival analysis (acoustic transmitter data)

Factors affecting bream and pike survival were examined using semiparametric Cox proportional hazards (CPH) regression (Cox 1972), the rationale being that this method allows for the analysis of time-varying covariates without making assumptions about the relationship between the hazard, or instantaneous rate of loss, and time (Therneau and Grambsch 2000). The hazard function $h(t)$ at time t was determined for a set of k covariates ($x_1, x_2, \ldots, x_k$) according to Murray (2006):

$$h(t) = h_0(t) \times \exp(\beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_k x_k)$$

where the coefficients β indicate the relative covariate effects and $h_0(t)$ is the nonparametric baseline hazard when the covariate vector x_1 = (0, 0, …, 0). The hazard ratio, $h_i(t)/h_j(t) = exp(\beta)$, is assumed to be independent of time.

The time-to-event interval represented time since release, and the event of interest was the last recorded acoustic detection or the last recorded detection prior to a signal becoming stationary, which indicated fish death or tag expulsion within range of a receiver. Individuals were right-censored from analyses if the last detection occurred within three months (for bream) or six months (for pike) of the study end date (i.e. their final detections were not recorded as losses). These species-specific censoring periods were necessary given the inter-specific behavioural differences of the fish, with bream tending to have much larger home ranges and higher vagility than pike (Koed et al. 2006, Gardner et al. 2013), and thus having greater probabilities of detection. Given these substantial differences in the behaviours of the two species, their data were also modelled separately. The time-constant predictors tested were fish length (cm; at capture), fish sex, sampling location (Upper Bure, Lower Bure, Thurne, Ant) and tagging date (Julian day of tagging). The time-varying covariates tested were water temperature, year and day of year (Julian day, representing seasonality). Non-linear relationships between the hazard and day of year, as well as tagging date, were accommodated using the pspline() function within the coxph() function of R's *survival* package (Therneau 2020). This allowed for smoothing using a 'p-spline' basis, while degrees of freedom were optimised by

minimising the corrected Akaike's Information Criterion (AIC) value (Hurvich et al. 1998, included in the package). In addition, robust variances were computed by clustering daily observations according to fish ID.

Covariates were initially parameterised separately in univariate models and compared to the 'null model' using AIC. Any covariates resulting in a reduction in AIC were retained for further comparison in multivariate models (Appendix 2, Table A2.1). Models incorporating and comparing the effects of fish sex were performed on reduced datasets due to missing data (as sex determination for 11 bream and one pike was considered unreliable; Appendix 2, Table A2.1). Given that fish sampling was not randomised in time and space, sampling location and tagging date were not modelled together to avoid collinearity. Bream length also differed significantly by sampling location (ANOVA: $F_{3,177} = 6.84$, $p < 0.001$; Table 3.1) and was thus modelled separately from sampling location and tagging date. Models incorporating the effects of both temperature and day of year were also disregarded. Models with $\Delta AIC \leq 2$ were considered to have strong support alongside the best-fitting ($\Delta AIC = 0$) model (Burnham and Anderson 2002), provided they were not more complex versions of nested models with greater AIC support (Richards et al. 2011). The proportional hazards assumption was verified for the best-fitting models by visual inspection of the Schoenfeld residual plots for departures from a horizontal (uncorrelated) trend. All statistical analyses were conducted using R 3.6.2 (R Core Team 2019).

3.3.4 Proportion of days detected (acoustic transmitter data)

The proportion of days detected was calculated for each fish by dividing the number of days on which acoustic detections were recorded by either the total number of days between the release date and the final detection (if fish were lost from the acoustic array) or by the total number of days between the release date and the study end date (if fish were right-censored from analyses).

3.3.5 Fate of fish lost from the acoustic array (PIT data)

An additional application of the multi-method, double-tagging approach was the interrogation of PIT data to identify any active fish that had been lost from the acoustic array. PIT-detected fish were classified according to their acoustic telemetry status (ATS); 'Active' or 'Lost'. 'Active' fish were detected by their PIT tag prior to disappearing from the acoustic array. 'Lost' fish were detected by their PIT tag after they had been considered as lost due to inactive or stationary acoustic signals. Binomial generalised linear models tested the effects of fish length (cm; at capture) and sex on ATS ('Active' = 0; 'Lost' = 1), with models compared to the null using AIC.

3.4 Results

3.4.1 Survival analysis (acoustic transmitter data)

A total of 181 bream were acoustically tracked for between 0 and 725 days (Table 3.1a), with 124 lost to the study. Of these, only 2 bream (1 %) moved outside the monitored area (last detected at receivers on the edge of the array). The surviving 57 bream were detected within three months of the study end-date and were therefore right-censored in statistical analyses. On average, bream were detected on 22 – 84 % of days, with those sampled and released in the River Ant detected the least frequently (Table 3.1a).

The predicted cumulative probability of bream survival to one year post-release was 0.61 (95% CI: 0.48 - 0.78; Figure 3.2). All covariates in the bream CPH univariate models, except fish sex, resulted in reduced AIC compared to the null model (Appendix 2, Table A2.1). The best-fitting CPH model predicting bream survival (ΔAIC = 0) retained nonlinear effects of tagging date and day of year, as well as a linear effect of year (Table 3.2a). The relative hazard (rate of loss) of bream was 7 to 21 times lower for individuals sampled in April than those sampled during the autumn or winter (Figure 3.3a). In addition, the hazard peaked at Day 156 (6th June in the calendar), at approximately 64 times the rate at Day 0 (1st January; Figure

3.3b). Although Year 2 was associated with an increased rate of loss compared to Year 1 ($\beta > 0$; Table 3.2a), uncertainty was high, with the confidence interval of the estimated hazard ratio (exp(β)) overlapping 1.0 (HR = 2.40; 95% CI: 0.67 - 8.63). Furthermore, under the selection criteria, the model incorporating nonlinear effects of day of year and tagging date, but without year, received strong support (ΔAIC = 0.85; Appendix 2, Table A2.1), indicating year was a relatively weak predictor of bream survival (Appendix 2, Table A2.2; Figure A2.1).

There were 45 pike that were acoustically tracked for between 4 and 727 days (Table 3.1b). Of these, 22 were lost to the study, with only 2 (4 %) having moved outside the monitored area. Thus, 23 pike were right-censored due to detections within six months of the study end-date. Pike were detected on 20 - 81 % of days, with mean values for each sampling location generally similar to those for bream (Table 3.1).

The overall cumulative probability of pike survival to one year post-release was predicted at 0.80 (95% CI: 0.66 - 0.96; Figure 3.2). In the pike CPH models, fish sex and a nonlinear effect of day of year improved model fit relative to the null model, and both covariates were retained in the best model (Table 3.2b; Appendix 2, Table A2.1). Relative rate of loss reached a maximum at Day 89 (31st March), at approximately 18 times the rate at Day 0 (Figure 3.3c). A second, smaller peak was observed at Day 290 (18th October), although confidence intervals widened toward the end of the year. In addition, male pike had a reduced rate of loss compared to females ($\beta < 0$; Table 3.2b), equating to a hazard ratio of 0.15 times that of females, although the confidence intervals for this value overlapped 1.0 (95% CI: 0.02 - 1.18).

Table 3.2. Coefficient estimates (β ± robust SE) for relevant covariates retained in the best-fitting CPH models predicting bream (a) and pike (b) survival.

Parameter	β	Wald's χ^2	d.f.	p
a) Bream				
Tagging date (linear)	-0.0002 ± 0.0012	0.12	1.00	0.73
Tagging date (nonlinear)		76.21	2.53	< 0.0001
Day of year (linear)	-0.0037 ± 0.0016	13.28	1.00	< 0.001
Day of year (nonlinear)		132.56	2.78	< 0.0001
Year	0.88 ± 0.70	1.80	1.00	0.18
b) Pike				
Day of year (linear)	0.0037 ± 0.0086	14.66	1.00	0.0001
Day of year (nonlinear)		94.12	2.77	< 0.0001
Sex:Male	-1.89 ± 1.03	3.25	1.00	0.071

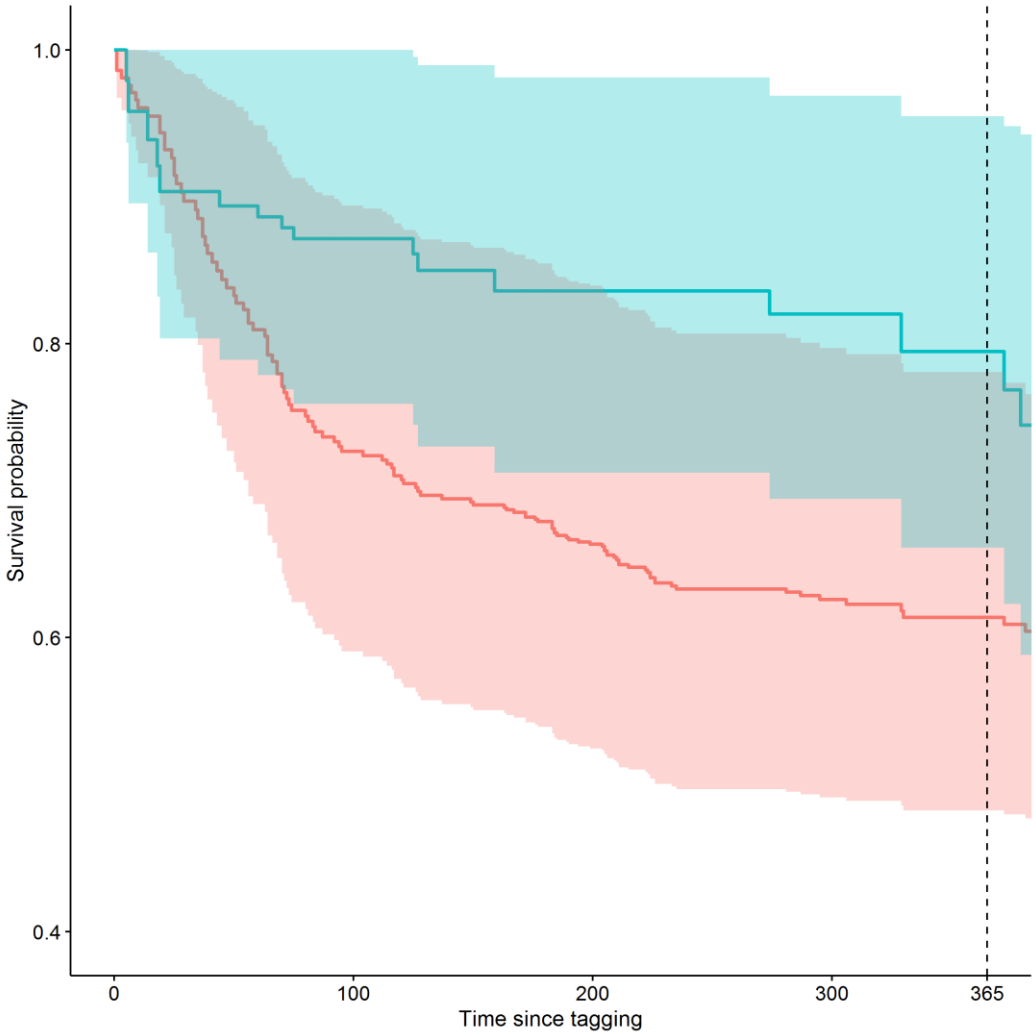

Figure 3.2: Predicted annual survival rates from bream *Abramis brama* (red/ light grey curves) and pike *Esox lucius* (blue/ dark grey curves) CPH models. Shaded regions represent 95 % CIs.

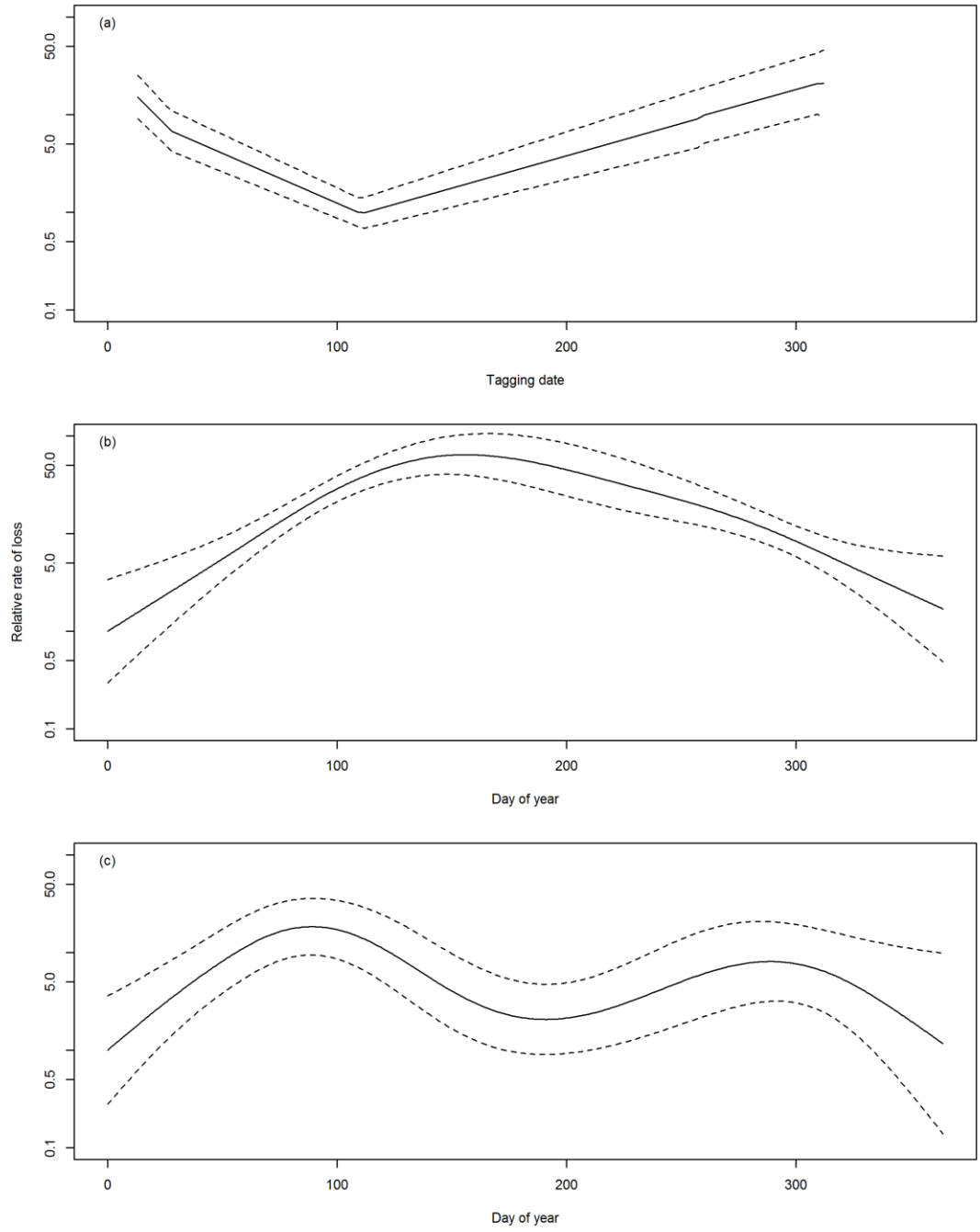

Figure 3.3: Nonlinear effects ('p-spline' smoothing) of tagging date (a) and day of year (b, c) on the rate of loss of bream *Abramis brama* (a, b) and pike *Esox lucius* (c) from the acoustic telemetry study according to the best-fitting CPH models. Hazards are relative to Day = 109 (a) and Day = 0 (b, c). X-axes represent time in Julian days.

3.4.2 Fate of fish lost from the acoustic array (PIT tag data)

The PIT antennae detected a total of 18 bream (Table 3.1). Of these, six fish (33 %) had previously been classified as 'Lost' from acoustic tracking (Table 3.3), providing evidence against their mortality. Half of those classified 'Lost' were due to stationary acoustic signals, suggesting acoustic tag expulsion rather than a transmission failure. The duration of acoustic tracking of 'Lost' fish, prior to a signal becoming inactive or stationary, ranged from 37 to 215 days, and final detections all occurred during late spring or early summer (Table 3.3), which corresponds with the trend described in the bream CPH model (Figure 3.3b). The delay between the final acoustic detection and the first PIT detection ranged from 18 to 359 days and, during that period, 'Lost' fish travelled between 1 and 24 km (Table 3). Fish length was a poor predictor of acoustic telemetry status (increased AIC), but sex improved model fit compared to the null model (Table 3.4), with male bream more likely to be classified as 'Lost'. The PIT antennae did not detect any pike that had been implanted with an acoustic transmitter.

Table 3.3. Acoustic and PIT tracking details of common bream 'Lost' from the acoustic array, but subsequently detected on PIT antennae. Delay and distance travelled represent the period between the final acoustic detection and the first PIT detection.

Fish ID	Location and timing of sampling	Acoustic tracking duration (days)	Date of final acoustic detection	Date of first PIT detection	Delay (days)	Distance travelled (km)
3811	Upper Bure – April 2018	37	27 May 2018	17 May 2019	355	22
27268	Upper Bure – April 2018	73	2 July 2018	15 May 2019	317	1
28576	Upper Bure – November 2017	215	8 June 2018	2 June 2019	359	1
28577	Upper Bure – November 2017	206	30 May 2018	17 June 2018	18	4
30036	Upper Bure – April 2018	87	15 July 2018	18 May 2019	307	24
30039	Upper Bure – April 2018	56	14 June 2018	18 May 2019	338	14

Table 3.4. Estimated regression parameters (± SE), *z*-values and *p*-values for the best binomial GLM predicting acoustic telemetry status (ATS) of common bream. The model resulted in a reduction in AIC by 2.3 compared to the null model.

	Estimate	*z*	*p*
Intercept	-2.08 ± 1.06	-1.96	0.050
Sex:Male	2.30 ± 1.26	1.84	0.067

3.5 Discussion

The study revealed that post-tagging survival rates varied according to the time of year for both species, with rates of loss peaking during and following their respective spawning periods. The results also demonstrated an effect of tagging date on the survival of bream, with fish tagged just prior to their spawning period (April) having the highest survival rate. In contrast, the date of tagging did not influence pike survival, and pike have been successfully implanted with transmitters in their pre-spawning period in other studies (Jepsen et al. 2000), although this was not attempted here. However, sex was an important determining factor for pike, with males generally surviving longer than females.

3.5.1 Timing of tagging

Tagging fish during their reproductive periods is generally avoided, as it reduces the risk of damage to internal organs, which may be enlarged, and prevents unnecessary stress during a period characterised by higher energy costs (Jepsen et al. 2002, Krams et al. 2017). For example, tagging success was reduced in gravid female channel catfish (*Ictalurus punctatus*, Rafinesque) when compared to spent females and males (irrespective of their reproductive state) (Marty and Summerfelt 1986). Consequently, it was considered counterintuitive that survival rates were greater for bream sampled from spawning aggregations than those sampled during autumn or winter, especially given immune systems in another cyprinid fish, roach (*Rutilus rutilus*, L.) are compromised during reproduction (Krams et al. 2017). Nevertheless, tagging of roach during spawning also did not appear to cause adverse effects (Hulthén et al. 2014). This highlights the need for evaluations of fish recovery and healing to be conducted in different environments, and in relation to testing across internal (e.g. hormonal) and external (e.g. seasonal) gradients (Cooke et al. 2011).

3.5.2 Fate of bream

For bream that did not survive within the study (annual probability of 0.39), few individuals left the monitored area, but PIT data revealed some lost their acoustic

transmitter signal. As the spatial and temporal coverage of the PIT monitoring stations was relatively low in the study area, the contribution of acoustic signal loss to overall loss of bream from the study could have been underrepresented. Natural mortality rates (in absence of fishing pressure) for bream populations in northern Europe and China have been estimated at 0.13 to 0.26 $year^{-1}$ (Kompowski 1988, Ding et al. 2019). Although these estimates are not directly comparable to the rate here, they do suggest the rate of loss of tagged bream was higher than what might be expected by natural mortality alone.

The process by which bream were lost from the acoustic array but remained active on the PIT antennae is uncertain. Possible explanations for the loss of an acoustic signal include transmission failure and/ or detection failure. The stationary tags provide some evidence against transmission failure. While acoustic shadows and interference may cause temporary fluctuations in detection efficiency (Simpfendorfer et al. 2008, Huveneers et al. 2016), detection failure over prolonged periods of time (confirmed fish survival up to 359 days after acoustic signal loss) and across large sections of the receiver network (confirmed fish movement up to 24 km after acoustic signal loss) is also considered unlikely, especially given successful detection of conspecifics throughout this time and space. One further consideration is the possibility of tag expulsion. This was not observed directly, but in other species tags are often lost through the incision site or via a lesion in the body wall (Jepsen et al. 2002). Both mechanisms could have occurred here, although with increasing time since surgery, wound healing should be further advanced, making surgical loss unlikely and the latter more likely (e.g. bream tracked for > 200 days prior to signal loss).

Other fish species, including the cyprinid common carp (*Cyprinus carpio,* L.), are particularly susceptible to loss of acoustic and radio transmitters (Marty and Summerfelt 1986, Daniel et al. 2009). Yet, tag expulsion has not been previously considered in common bream, despite several completed studies using these methods (e.g. Gardner et al. 2013, Gardner et al. 2015b, Brodersen et al. 2019). The estimate of the proportion of bream losing their acoustic tag signal was dependent on bream retaining their PIT tag and therefore could be an underestimate if some individuals

expelled both tags. However, PIT tag retention is generally high in cyprinid fishes (Skov et al. 2005, Bolland et al. 2009), especially for males (Šmejkal et al. 2019), but with some exceptions, such as topmouth gudgeon (*Pseudorasbora parva,* Temminck & Schlegel; Stakėnas et al. 2009). For bream confirmed active by PIT telemetry, loss of acoustic signals occurred up to 215 days (> 6 months) post-tagging, but all incidents occurred in late spring or summer, suggesting some role of spawning activity and/ or elevated temperatures, as also suggested for tag losses in common carp (Daniel et al. 2009). In addition, male bream were more likely to experience acoustic signal loss that was then followed by a PIT tag detection, emphasising the need for long-term tag retention studies in this species. When conducted over a range of naturally fluctuating environmental conditions, these should be more insightful than studies focusing only on the initial days and weeks post-tagging and/ or which operate under artificial laboratory conditions. However, any wild study would require consideration of the need to recapture individuals in order to determine the mechanisms driving acoustic signal loss.

3.5.3 Fate of pike

The annual probability of pike loss due to mortality, acoustic signal loss or fish leaving the study area was estimated as 0.20 (from a survival probability of 0.80). In the literature, estimates for the natural mortality rate of adult pike vary widely and may exceed 0.50 $year^{-1}$, with males having similar or greater mortality compared to females (Kipling and Frost 1970, Haugen et al. 2007). While results here suggested a greater loss of females, prediction error was wide. A possible explanation is that male pike exhibit greater vagility than females (Haugen et al. 2007) and subsequently, the survival of females may have been underestimated due to their relatively sedentary behaviour (Koed et al. 2006). Nevertheless, the rate of loss of tagged pike appeared relatively low, indicating minimal impact of the tagging process.

No pike were detected via their PIT tags, therefore the proportion that died versus those that lost their acoustic signals (through tag failure, tag expulsion etc.) could not be estimated. However, other studies have suggested tag loss in the species in low.

For example, Jepsen and Aarestrup (1999) found no expulsion of internal radio tags after one year, and several recent studies that have utilised acoustic or radio telemetry to measure pike movements (for up to 18 months) have not reported evidence of tag loss (e.g. Jacobsen et al. 2017, Pauwels et al. 2017, Birnie-Gauvin et al. 2019). If the reason for signal loss was tag expulsion then differences in rates between the two species may be due to differences in morphology, where pike are more fusiform, with a wider body cavity than the laterally-compressed bream. Consequently, pressure on internal organs and at the incision site might have been lower in pike, limiting tag loss (Jepsen et al. 2002, Cooke et al. 2011). Notwithstanding, there was complete retention of dummy acoustic tags in the laterally-compressed bloater (*Coregonus hoyi*, Milner) (Klinard et al. 2018), suggesting that generalising about tag losses across morphological, taxonomic or behavioural groups should be done with caution.

3.5.4 Interpretation of survival

One fate not considered here is the possible consumption of tagged fish by aquatic predators (e.g. pike, otters), with the acoustic tags still appearing active in the study system. Elsewhere, this is typically identified by uncharacteristic changes in depth or horizontal space use (Klinard and Matley 2020, Villegas-Ríos et al. 2020), but given the nature of the study system (i.e. shallow and relatively spatially confined), the movements of bream or pike and their predators were considered difficult to distinguish. The use of new telemetry technology designed to definitively identify predation events (Halfyard et al. 2017) has revealed acoustic transmitters may be retained for substantial time in the guts of piscivorous predators (> 150 days; Klinard et al. 2019b), meaning survival may have been overestimated here. In addition, ghost tags (due to fish mortality or tag expulsion) can also travel independently within river systems, especially PIT tags during high flow events (Bond et al. 2019), although some may remain relatively stationary for long periods (Šmejkal et al. 2020). In the tidal River Bure system, while these movements could mask a mortality or tag loss event, the high flows that would be required to transport a tag are unlikely, usually being buffered by the wetland nature of the system that generally prevents large and sudden influxes of floodwater.

In summary, the results here demonstrated that the survival of fish that undergo intra-peritoneal implantation of transmitters varies by species, and within species it can vary by sex and the date of tagging. They also suggested that where fish failed to survive during the study period, this could be due to the loss of the acoustic tag signal (e.g. due to tag loss or tag failure), rather than actual mortality, with the additive mortality caused by the procedure and subsequent tag burden appearing negligible considering natural mortality rates. Moreover, the double-tagging approach was instrumental in revealing the subsequent activity of fish that had lost their acoustic signal. This method of distinguishing mortality from tag loss/ failure appears original, with no mention in a recent review of mortality assessments in acoustic telemetry research (Klinard and Matley 2020). However, it should always be considered in future fish tagging studies to assist assessments of post-tagging survival.

4 Dual-isotope isoscapes for predicting the scale of fish movements in lowland rivers

4.1 Abstract

Assessments of patterns of animal movements are important for understanding their spatial ecology. Geostatistical models of stable isotope (SI) landscapes ('isoscapes') provide a complementary tool to telemetry for assessing and predicting animal movements, but are rarely applied to riverine species. Often single isotope gradients in freshwater environments are insufficiently variable to provide high isoscape resolution at relatively fine spatial scales. This is potentially overcome using dual-isotope assignment procedures and thus the aim here was to apply single ($\delta^{13}C$) and dual ($\delta^{13}C$ and $\delta^{15}N$) isoscapes to assigning riverine fish to origin and predicting their movements. Using the River Bure, England, as the study system, the foraging locations of a small-bodied lowland river fish (roach *Rutilus rutilus*) of low vagility were predicted using their SI data and those of a common prey item (amphipods). These foraging locations were then compared to their capture locations, with the distance between these being their 'predicted displacement distance' (PDD). The results indicated significant enrichment of $\delta^{13}C$ and $\delta^{15}N$ with distance downstream in roach fin tissue and amphipods; roach bivariate isotopic niches were spatially variable, with no niche overlap between upstream and downstream river reaches. Furthermore, the dual-isoscape assignment procedure resulted in the lowest PDDs for roach and therefore minimised model error. The dual isoscape approach was then applied to determining the PDD of individual common bream *Abramis brama*, a larger, more vagile species, with these data then compared against the subsequent spatial extent of their movements recorded by acoustic telemetry. The PDD of common bream was a significant predictor of the spatial extent of their subsequent movements recorded by acoustic telemetry, although it was less able to predict the direction of displacement. This first probabilistic assignment to origin for riverine species using a dual-isotope isoscape technique demonstrated that where the required spatial resolution of animal movements in freshwater is moderately broad (5 – 10 km), dual-isotope isoscapes can provide a reliable alternative or complementary method to telemetry.

4.2 Introduction

Documenting and understanding the scales of animal movements can be inherently challenging, yet inter- and intra-specific variation in movement distances can provide essential information on the availability and utilisation of functional habitats (Mayor et al. 2009). Whilst electronic tags provide the opportunity to directly measure animal movements (e.g. Hussey et al. 2015), issues remain regarding their application in the aquatic environment, including the limited battery life of transmitters, the adverse physiological and/ or behavioural effects of tagging on individuals, elevated study costs, and the limited detection range of transmitters across broad spatial scales (Brownscombe et al. 2019).

An alternative to telemetry is the inference of movements using intrinsic chemical markers, such as contaminants, inorganic trace elements and/ or isotopes (Hobson and Wassenaar 2008). Individuals acquire distinct chemical profiles according to their geographic location, which can be permanently retained in metabolically inert tissues (e.g. hair, feathers, fish otoliths; Gillanders 2005, Hobson and Wassenaar 2008). When associated with the timescales of exposure, these chemical data can be used to reconstruct animal movements. For example, otolith strontium:calcium (Sr:Ca) ratios are widely used as a proxy for salinity gradients to examine freshwater-marine habitat shifts of fishes (Gillanders 2005, Quinn et al. 2014). Also, in freshwaters, strontium isotope ratios (^{87}Sr:^{86}Sr) are commonly used to classify organisms to a watershed origin due to their association with the underlying geology (Kennedy et al. 2005, Duponchelle et al. 2016).

The chemical profiles of metabolically active tissues, such as muscle, can also provide information regarding an animal's geographic location through their representation of diet over varying timeframes (Hobson and Wassenaar 2008). Typically, the stable isotope ratios of 'light' elements, such as carbon ^{13}C:^{12}C (i.e. $\delta^{13}C$) and nitrogen ^{15}N:^{14}N (i.e. $\delta^{15}N$) are employed as intrinsic markers that reflect geochemistry, as well as trophic dynamics (Peterson and Fry 1987). In fishes, stable isotope analysis (SIA) has utilised a multitude of tissue types, from mucus (Winter et al. 2019) to eye lenses (Wallace et al. 2014), with those sampled nonlethally

providing a marked advantage in situations where lethal methods are either not permitted or are undesirable.

The successful application of chemical tracers to inferring animal movements requires detailed knowledge of the specific elemental/ isotopic variation in the environment. For stable isotopes (SI), geostatistical models of isotopic landscapes ('isoscapes') can be developed to 'assign' tissue SI signatures to their most probable geographic source (Vander Zanden et al. 2018). This isotopic tracking technique has been routinely applied to birds (e.g. Bowen et al. 2005) and, increasingly, to terrestrial mammals, insects and marine fauna (Trueman et al. 2012, Voigt et al. 2012, Hobson et al. 2018). However, its use is rare for freshwater species (but see Brennan and Schindler 2017), perhaps due to relatively poor resolution of single isotopes at moderately fine spatial scales. The development of multi-isotope isoscapes has helped overcome this for terrestrial and marine tracking, enabling more spatially explicit predictions of movements and so advancing the geographic assignment process (Hobson et al. 2012, Vander Zanden et al. 2015a). Nevertheless, use of multi-isotope isoscapes to predict fish movements is rare, with the only example being a dual-isoscape ($\delta^{18}O$, $\delta^{13}C$) for assessing Atlantic salmon *Salmo salar* movements in the Baltic Sea (Torniainen et al. 2017).

Within river basins, there tends to be a gradual enrichment in $\delta^{13}C$ with distance from the source to sea (Peterson and Fry 1987). This geochemical gradient is reflected in the tissues of locally foraging organisms and has been applied to infer the foraging ranges of fishes using simple regression statistics (Cunjak et al. 2005, Rasmussen et al. 2009, Bertrand et al. 2011). In contrast, $\delta^{15}N$ tends to be less spatially variable, although enrichment can occur along salinity gradients (Quinn et al. 2014) and due to disturbance from anthropogenic activities (Harrington et al. 1998, Kennedy et al. 2005). Correspondingly, the combined application of $\delta^{13}C$ and $\delta^{15}N$ can reveal distinct isotopic niches within freshwater habitats (Kennedy et al. 2005). These isotopic markers could potentially be used in dual isoscapes for predicting finer scale movements of vagile species, with isoscape-derived predictions then complementing any movement data available from telemetry methods, as demonstrated by Seminoff et al. (2012) in their assessment of movements of

leatherback sea turtles *Dermochelys coriacea* in the Pacific Ocean. As recapturing tagged animals can be difficult in many environments, the complementary use of isoscapes and telemetry can be reliant on stable isotope data collected from animals at the time of tagging, providing the opportunity for testing whether isotope data collected at the time of tagging can be a good predictor of the subsequent movements of individuals (Harrison et al. 2017).

The aim here was to apply isoscape models to predicting the movements of two lowland river fish species. Firstly, single ($\delta^{13}C$) and dual isoscape ($\delta^{13}C$ and $\delta^{15}N$) models predicted the foraging locations of a small-bodied lowland river fish of relatively low vagility, based on their SI data and that of a common prey resource. Post-hoc measurements of the predicted displacement distance to capture location were used to assess model performance. The dual isoscape models were then applied to predicting the foraging locations of a larger-bodied species of relatively high vagility in the same system. As these fish were sampled non-lethally for their SI data, the predicted displacement distances to capture locations were then compared with their actual movements, as detected using acoustic telemetry over a 12-month post-sampling period. Thus, these data also enabled evaluation of the extent to which SI data collected at tagging predicts the spatial extent of subsequent fish movements.

4.3 Methods

4.3.1 Study species

Roach (*Rutilus rutilus*), a common lowland river fish of the Cyprinidae family found across Eurasia, that rarely exceeds lengths of 300 mm (Tarkan and Vilizzi 2015, Ruiz-Navarro et al. 2016), was the small-bodied fish of relatively low vagility used in the study. The larger bodied fish was common bream (*Abramis brama*), a cyprinid that has a similar natural range to roach, but with individuals regularly attaining lengths > 450 mm (Lyons and Lucas 2002). Although zooplanktivorus in juvenile life-stages, the diets of riverine populations of both fishes tend to be dominated by macro-invertebrates as their body size increases (Persson and Brönmark 2002, Hjelm et al. 2003). For roach, other than during spawning in spring when populations can

move considerable distances to spawning grounds, the spatial extent of habitat use rarely exceeds 5 km (e.g. Baade and Fredrich 1998). By contrast, common bream are more vagile, performing both spawning and seasonal habitat shifts of up to 60 km (Whelan 1983, Gardner et al. 2013).

4.3.2 Study system

The study system was the River Bure in eastern England. It is 87 km in length, flows south-east towards Breydon Water estuary at Great Yarmouth, and has a mean discharge of 3 $m^3 \cdot s^{-1}$ into the North Sea (Figure 4.1). The Bure and its tributaries, the Rivers Ant and Thurne, form the northern area of the Broads National Park, a wetland of significant ecological importance (Natural England 2020; Figure 4.1). The area is characterised by multiple small shallow lakes termed 'Broads' (medieval peat diggings). As the landscape is generally flat, the catchment is tidal for approximately 45 km inland, with water levels fluctuating daily by about 10 cm towards the upstream limit of the study area (Figure 4.1). At Acle, approximately 18 km from the river mouth (Figure 4.1), conductivity (as a measure of salinity) can fluctuate between 1,000 and 50,000 $\mu S \cdot cm^{-1}$, with major saline incursions occurring during tidal surges and/ or low flows, generally in winter (Clarke 1990). As the upper limit of saline incursion is believed to be at Horning (Figure 4.1; Clarke 1990), this location was used as the boundary between the 'upper' (minimal saline influence) and 'lower' (stronger saline influence) river reaches within the study area. The upper reaches were approximately 25 m wide with depths to 1.5 m, while in the lower reaches channel widths increased to >40 m, with depths of over 3 m. Across the two reaches, the fish assemblage has limited diversity, being dominated by roach and common bream.

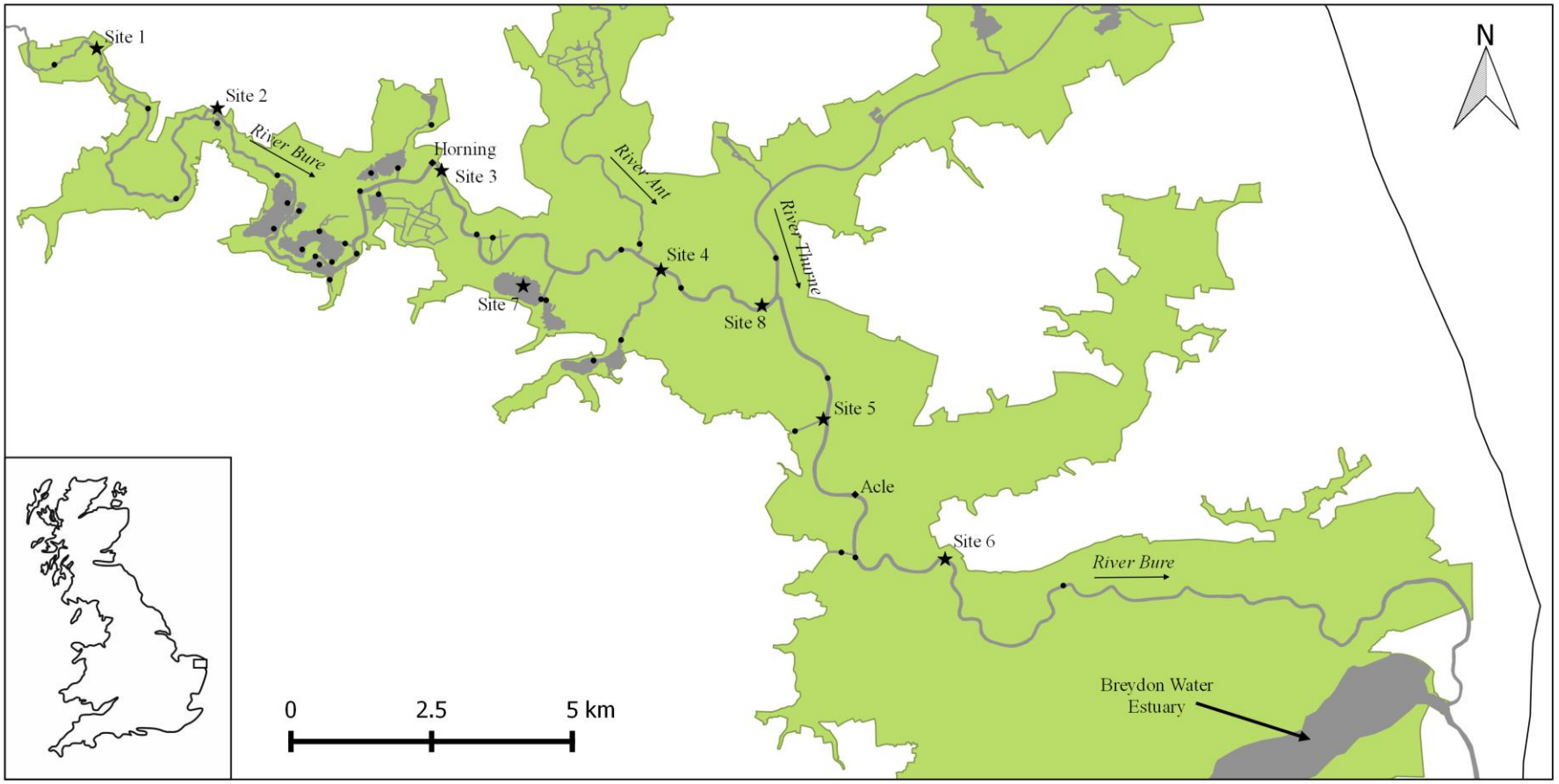

Figure 4.1: Map of the River Bure study system, eastern England, showing sample sites (stars) and locations of acoustic telemetry receivers (circles). The boundary between the upper and lower river reaches is at Horning. The area of the Broads National Park is shaded green. All waterways pictured are tidal. Channel width not to scale.

A fixed array of 36 acoustic receivers (Vemco, VR2W) was installed throughout the River Bure prior to fish sampling. These were distributed over 37 km of main river channel and associated off-channel habitats (Figure 4.1), and continuously monitored fish movements for the duration of the study. Receivers were placed in the channel margins at approximately mid-water depth. Detection ranges were variable, dependent on environmental conditions (Chapter 2), however very rarely fell below channel width distance.

4.3.3 Fish sampling and acoustic tagging

The sampling period was 11 September to 3 October 2018, towards the end of the summer growth season for both fishes in the river. Roach and their putative prey resources were sampled across two sites in the upper river reach (Sites 1 and 2) and four sites in the lower reach (Sites 3 to 6; Figure 4.1). Roach sample sizes were a minimum of 9 fish per site (N = 60). In addition, 19 common bream were sampled from three sites in the lower river reach (Sites 4, 7 and 8; Figure 4.1). Due to heavy boat traffic, sampling by typical fish capture methods (e.g. electric fishing, seine netting) was not feasible and angling was used as an alternative. All captured fish were identified to species, measured (fork length, nearest mm) and a biopsy of the pelvic fin taken and frozen for storage. Captured roach were of lengths 85 to 223 mm (mean ± SD = 145 ± 32 mm) and common bream 321 to 503 mm (mean ± SD = 411 ± 47 mm). At these sizes, the diet of both fishes tends to focus on macro-invertebrates, including amphipods (Persson and Brönmark 2002, Hjelm et al. 2003). Amphipods also dominated samples of macro-invertebrates collected from littoral habitats, including the invasive *Dikerogammarus villosus*. Thus, amphipods were used as the putative prey of both fishes in subsequent analyses.

The sampled common bream were surgically implanted with internal acoustic tags, sourced from Vemco (V13; 69 kHz; length 36 mm × diameter 13 mm; 6.0 g weight in water; random transmission interval around 120 s; estimated battery life 1200 days; N = 11) and Thelma Biotel (ID-LP13; 69kHz; length 28 mm × diameter 13 mm; 5.5 g weight in water; random transmission interval around 120 s; estimated battery life 1400 days; N = 8). Surgical instruments were disinfected in iodine

solution prior to each procedure and fish scales were removed from the incision site to aid scalpel and suture entry. Tags were inserted ventrally and anterior to the pelvic fins and incisions were closed with a single suture and wound sealer. All regulated procedures were performed whilst the fish were under general anaesthesia (Tricaine methanesulfonate, MS-222), according to the UK Home Office licence 70/8063 and after ethical review. All fish were returned alive to the river following their postoperative recovery and return to normal behaviour.

4.3.4 Stable isotope analysis (SIA)

Fish and amphipod samples were rinsed in distilled water, dried at 60 °C to constant weight and then analysed for $\delta^{13}C$ and $\delta^{15}N$ (‰) at the Cornell University Stable Isotope Laboratory, New York, USA, where they were ground to powder and weighed precisely to 1000 µg in tin capsules. The samples were analysed on a Thermo Delta V isotope ratio mass spectrometer (Thermo Scientific, USA) interfaced to a NC2500 elemental analyser (CE Elantach Inc., USA). Lipid correction was not performed, given C:N ratios indicated low lipid content across all taxa (< 3.5).

For macro-invertebrates, amphipods of the family Gammaridae were the main group analysed as these dominated the samples. One SI sample was comprised of up to five individuals and a minimum of four samples were collected for each site (N = 34), except for Site 2 where sampling for Gammaridae was unsuccessful. For SIA, *D. villosus* were kept separate from *Gammarus* spp. Where *Gammarus* spp. and *D. villosus* were sampled from the same site, isotopic differences between the groups were not significant for $\delta^{13}C$ (*t*-test; Site 4: $t_6 = 1.31$, $p = 0.24$; Site 5: $t_5 = 0.47$, $p = 0.66$). For $\delta^{15}N$, there was no difference at Site 5 ($t_5 = 1.29$, $p = 0.25$), but a significant difference occurred at Site 4 ($t_6 = 2.80$, $p = 0.03$), although the difference of 0.84 ‰ was not considered biologically relevant in the context of $\delta^{15}N$ fractionation between consumer and prey being in the region of 3.0 to 3.4 ‰ (e.g. Post 2002). Thus, for subsequent analyses, *Gammarus* spp. and *D. villosus* SI data were combined as ‘amphipods’.

4.3.5 Data analyses

Bivariate isotopic niches for the roach samples from each site and reach were visualised using 95% confidence ellipses of the bivariate means, corrected for small sample sizes, using the R package SIBER (Jackson et al. 2011). Then, the R package IsoriX (Courtiol et al. 2019) was used to create isoscape models for expected $\delta^{13}C$ and $\delta^{15}N$ of amphipod and roach fin tissue in the river using the SI data from Sites 1 to 6. The geostatistical 'mean model' was a linear mixed-effects model (LMM), with linear river distance (km from source; DIST) and biotic group (amphipod/roach; GRP) as fixed effects, plus sample site as a random effect. To account for spatial autocorrelation, an additional Matérn correlation function (Matérn 1960) was included in the mean model as a random effect. A dendritic approach to geostatistics (Brennan and Schindler 2017) was not considered appropriate due to the tidal nature of this system, which buffers the downward transport of organic matter, including at tributary junctions. In a further gamma Generalised LMM (GLMM) (the 'residual dispersion model'), the variance of the residual error in the mean model was assumed to be spatially structured according to the random effects of sample site and a Matérn correlation structure. A detailed account of the model structure is available in Courtiol and Rousset (2017). The inclusion of an interaction term (DIST*GRP) in the best fitting mean models for $\delta^{13}C$ and $\delta^{15}N$ was determined by the minimisation of conditional AIC values (cAIC; Vaida and Blanchard 2005), provided by the *AIC* function in package IsoriX (Courtiol et al. 2019).

The single and dual-isoscapes were generated for amphipods and roach using a structural raster of the study system (approx. cell resolution = 8 m^2), containing linear river distance data (distance from source) measured to the nearest km. For each raster cell (r), the predicted mean and residual variance for $\delta^{13}C$ (μ_C; σ^2_C) and $\delta^{15}N$ (μ_N; σ^2_N) were derived directly from the mean model outputs. To assign the single-isotope ($\delta^{13}C$) value of a test sample with its predicted foraging location, a spatially explicit univariate normal probability density function was calculated according to:

$$P(x|r) = \frac{1}{\sqrt{2\pi}\sigma_{C_r}} exp(-\frac{\left(x-\mu_{C_r}\right)^2}{2\sigma^2_{C_r}})$$

Alternatively, to assign the dual-isotope ($\delta^{13}C$ and $\delta^{15}N$) values of a test sample with its predicted foraging location, a spatially explicit bivariate normal probability density function was calculated according to:

$$P(x,y|r) = \frac{1}{2\pi\sigma_{C_r}\sigma_{N_r}\sqrt{1-\rho^2}} exp\left(-\frac{z}{2(1-\rho^2)}\right)$$

where

$$z = \frac{(x-\mu_{C_r})^2}{\sigma_{C_r}^2} - \frac{2\rho(x-\mu_{C_r})(y-\mu_{N_r})}{\sigma_{C_r}\sigma_{N_r}} + \frac{(y-\mu_{N_r})^2}{\sigma_{N_r}^2}$$

In the equations, x and y denote the $\delta^{13}C$ and $\delta^{15}N$ values of the test sample, respectively, while r, μ_C, σ^2_C, μ_N, and σ^2_N are as defined previously. The correlation of x and y is defined by ρ and was obtained from the mean correlation of $\delta^{13}C$ and $\delta^{15}N$ at each sample site. The predictive power of single- and dual-isotope signatures in identifying fish foraging areas was assessed using a 5-fold cross validation technique. Data were split into five mutually exclusive subsets, each containing 12 fish (20%), with stratified sampling from each sample site used to account for the hierarchical data structure (Koper and Manseau 2009). With each fold, four subsets were used as training data to fit the roach isoscape models and one as testing data to predict the foraging locations of each fish (value of r for which $P(x|r)$ or $P(x,y|r)$ was maximised). The linear river distance between this raster cell and the capture location of each fish was determined as the 'predicted displacement distance' and used to represent model error.

As the ecological niches of adult roach and common bream overlap considerably, the roach dual isoscape was assumed a suitable baseline for the geographic assignment of bream. Diet-tissue isotopic fractionation was also assumed to be similar for the two fishes, such that a rescaling of the baseline was not required. Bream were assigned to their predicted foraging locations using the method above, with the predicted displacement distance from their respective capture sites also calculated as per roach. In addition, acoustic telemetry data were collected for up to one year from 25 September 2018 (7 days post-release), with analyses using individual fish that were detected for at least nine months post-release as this enabled their movements to be tracked during their 2019 growth season (Appendix 3, Table A3.1). Any

individual spending substantial time (> 50 %) outside of the study area (e.g. in tributaries; Figure 4.1) was removed from the analysis. Weighted linear regressions assessed whether isotopic displacement could predict the scale and directionality of fish movements the following year, measured as the maximum displacement from the capture site evidenced by acoustic telemetry, and weighted according to the proportion of time spent within 8 km (see Results) of this location. Standard linear regressions examined whether fish length was a factor determining $\delta^{13}C$, $\delta^{15}N$ or maximum displacement recorded by telemetry. All analyses were conducted in R 3.5.3 (R Core Team 2019).

4.4 Results

4.4.1 Stable isotope data of roach and amphipods

The isotopic signatures of roach and amphipods revealed a similar range and enrichment pattern ($\delta^{13}C$ amphipods: -32.4 to -26.8 ‰; $\delta^{13}C$ roach: -32.0 to -23.8 ‰; $\delta^{15}N$ amphipods: 11.0 to 15.2 ‰; $\delta^{15}N$ roach: 12.3 to 19.1 ‰). Using 95% confidence ellipses of the bivariate means, dual-isotopic profiles ($\delta^{13}C$ and $\delta^{15}N$) for roach sampled across Sites 1 to 6 revealed varying levels of niche overlap, with an overall enrichment of both isotopes with distance downstream (Figure 4.2a). When grouped into the upper and lower river reaches, the two ellipses did not overlap (Figure 4.2b).

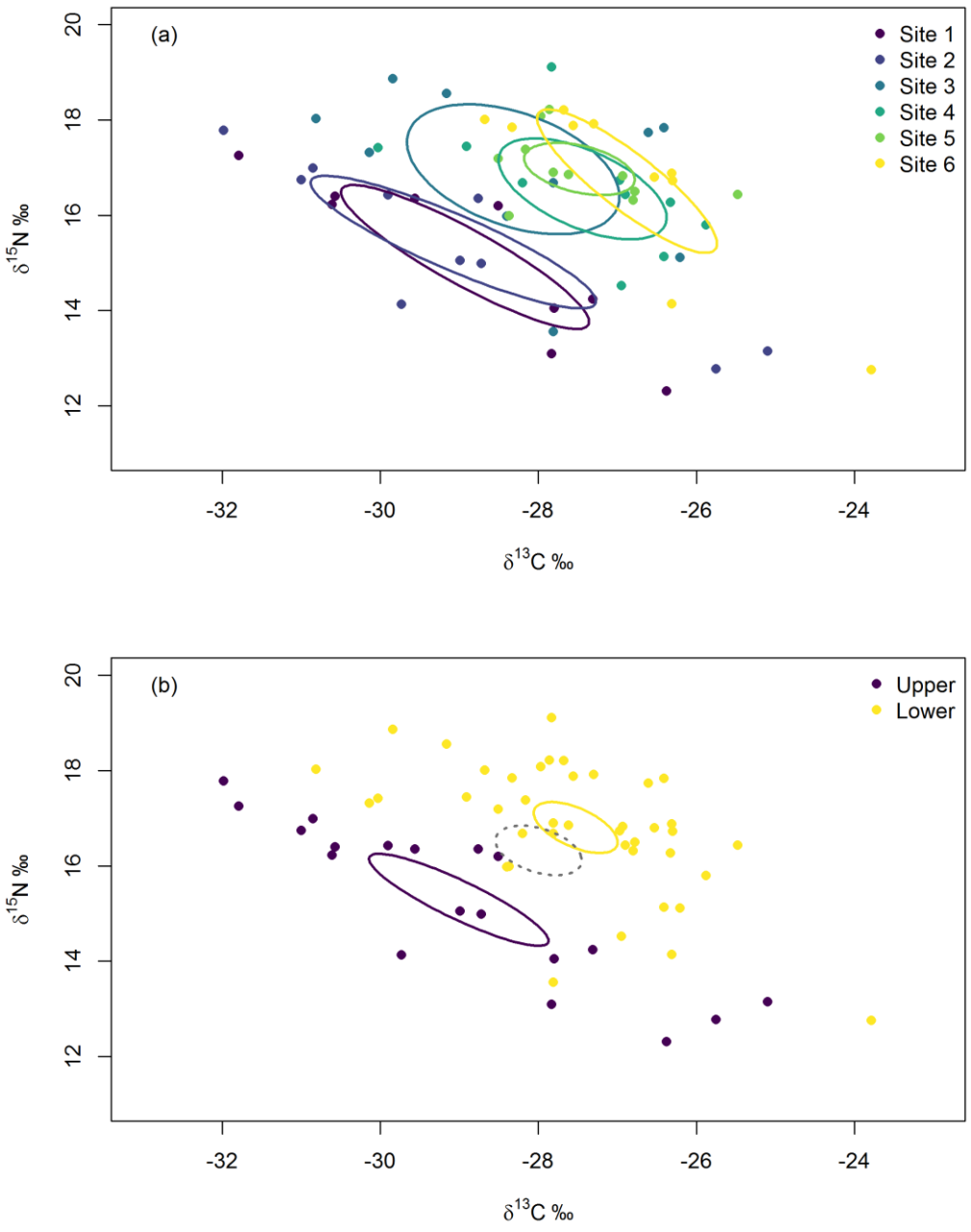

Figure 4.2: Stable isotope biplot and associated 95 % confidence ellipses of the bivariate means for roach subpopulations grouped according to sample site (a) and river reach (b). The ellipse for all data combined is given in (b) as a dark grey dotted line.

4.4.2 Isoscapes and predicted roach foraging areas

In the geostatistical models, the best-fitting $\delta^{13}C$ mean model retained both river distance and biotic group as fixed effects, with a predicted enrichment of 0.08 ‰ per km and an amphipod-roach fractionation of 1.56 ‰ (Table 4.1a). Similarly, the best-fitting $\delta^{15}N$ mean model retained both river distance and biotic group as fixed effects, with a predicted enrichment of 0.06 ‰ per km and an amphipod-roach fractionation of 2.93 ‰ (Table 4.1b). Interaction terms were not retained in either of the best models predicting $\delta^{13}C$ and $\delta^{15}N$. The isoscapes resulted from joint predictions stemming from both fixed and random effects (Figure 4.3). Residual variance was greatest in the upper reaches of the river for both $\delta^{13}C$ and $\delta^{15}N$ isoscapes (Figure 4.3).

Cross-validation of the univariate and bivariate probability density functions revealed that 30 % of roach were geographically assigned to predicted foraging locations within 5 km of their capture locations using a single-isotope signature, compared to 40 % using a dual-isotope signature (Figure 4.4). Mean predicted displacement distance (or model error), irrespective of directionality, was 11.4 km using a single-isotope signature versus 8.2 km using a dual-isotope signature, although this varied spatially (Table 4.2). For roach captured at Sites 1 and 2, the dual-isotope assignment procedure performed best when predicting the river reach of foraging (correctly assigned to upper reach: single-isotope: 63 %; dual-isotope: 95 %). By contrast, for roach captured at Sites 4 to 6, the single-isotope assignment procedure performed best when predicting the river reach of foraging (correctly assigned to lower reach: single-isotope: 81 %; dual-isotope: 74 %). Site 3 was situated close to the reach boundary, resulting in 60 % correctly assigned to the lower reach for both single- and dual-isotope procedures.

Table 4.1: Linear mixed-effects model coefficient estimates (± SE) for the geostatistical 'mean model' fixed effects predicting $\delta^{13}C$ (a) and $\delta^{15}N$ (b). Linear river distance = DIST. Biotic group = GRP. Estimates for the amphipod category are represented by the intercept.

(a) $\delta^{13}C$

Model	Intercept	DIST	GRP:Roach	DIST*GRP:Roach	ΔcAIC
1	-33.43 ± 0.82	0.08 ± 0.01	1.56 ± 0.30	-	0.00
2	-34.33 ± 1.46	0.09 ± 0.03	2.83 ± 1.73	-0.02 ± 0.03	1.44

(b) $\delta^{15}N$

Model	Intercept	DIST	GRP:Roach	DIST*GRP:Roach	ΔcAIC
1	9.94 ± 2.40	0.06 ± 0.05	2.93 ± 0.27	-	0.00
2	10.35 ± 2.72	0.06 ± 0.05	1.89 ± 1.54	0.02 ± 0.03	1.53

Table 4.2: Mean predicted displacement distances (mean error; km) (± SD) following the single- and dual-isotope geographical assignment procedures for roach, both grouped by sample site and combined across the study system.

Location	Single-isotope ($\delta^{13}C$)	Dual-isotope ($\delta^{13}C$ & $\delta^{15}N$)
Site 1 (Upper Reach)	15.4 ± 13.6	4.3 ± 3.7
Site 2 (Upper Reach)	12.5 ± 9.5	7.0 ± 6.6
Site 3 (Lower Reach)	14.0 ± 6.1	10.9 ± 7.3
Site 4 (Lower Reach)	11.2 ± 6.8	10.2 ± 4.4
Site 5 (Lower Reach)	6.5 ± 4.1	5.1 ± 4.8
Site 6 (Lower Reach)	9.9 ± 6.9	11.7 ± 7.0
All sites	11.4 ± 8.4	8.2 ± 6.3

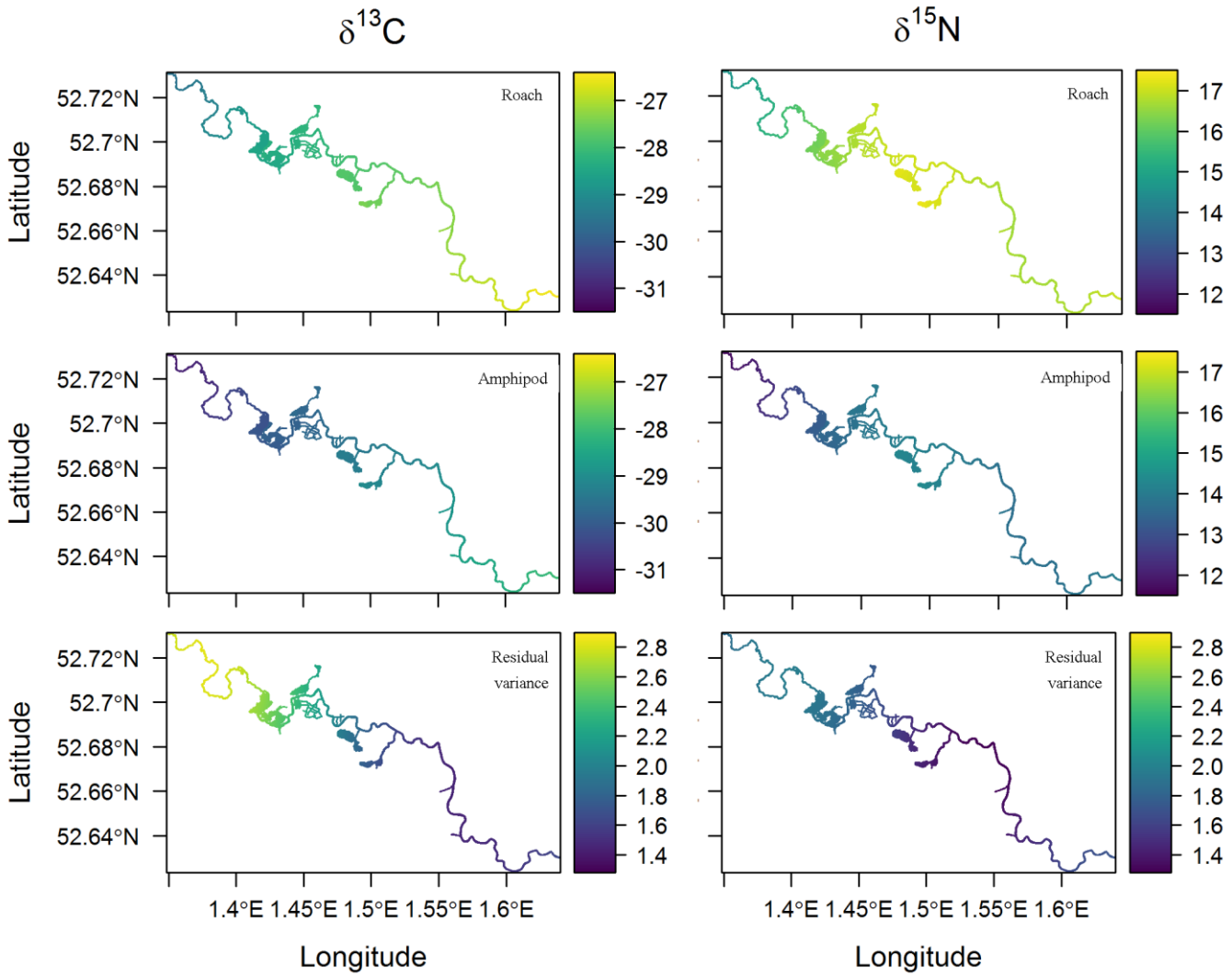

Figure 4.3: $\delta^{13}C$ (left) and $\delta^{15}N$ (right) isoscapes based on best-fitting LMMs for roach fin tissue (top) and amphipods (middle) in the River Bure. Residual variance (bottom) is also displayed. Channel width not to scale.

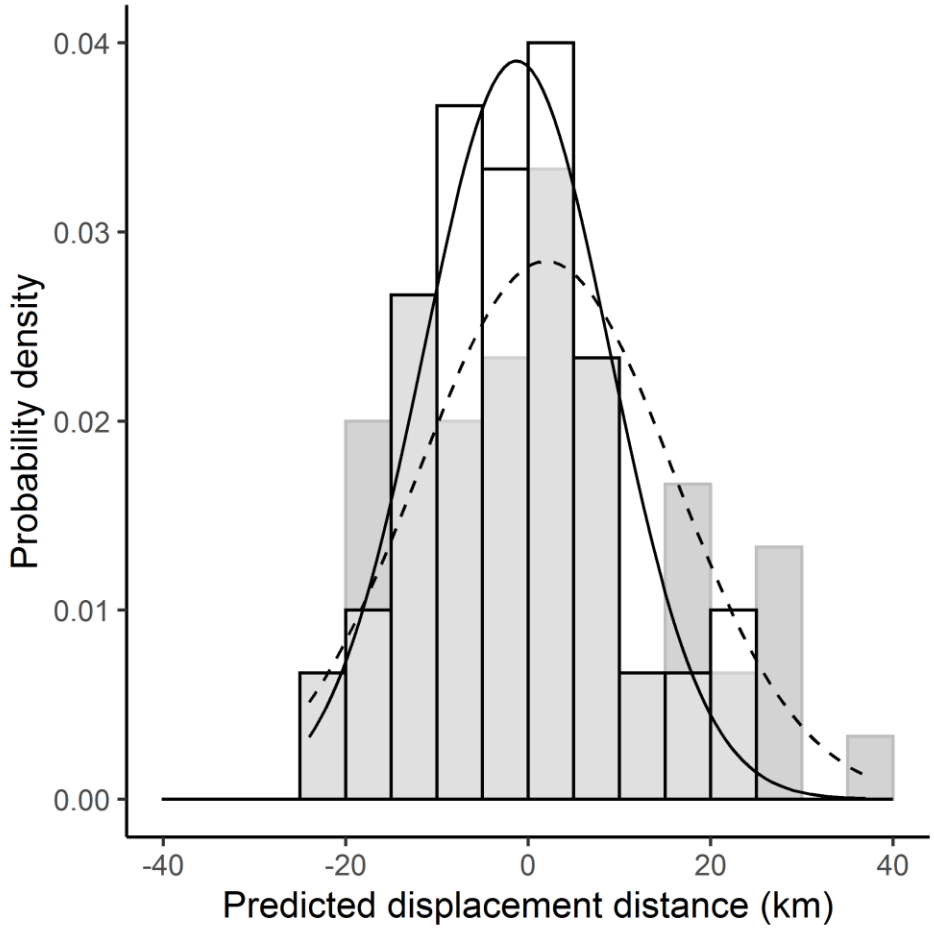

Figure 4.4: Probability density of predicted displacement distances (i.e. geographic assignment errors) for roach using single- (shaded) and dual-isoscapes (white). Normal probability density functions are displayed for single- (dashed line; mean ± SD = 2.37 ± 13.67) and dual-isotope errors (bold line; mean ± SD = -0.95 ± 9.95).

4.4.3 Common bream tracking and predicted foraging areas

Bream were acoustically tracked from 12 to 365 days (mean ± 95 % CI = 242 ± 51 days), with eight individuals detected for at least nine months (274 days), including two captured at Site 4, three captured at Site 7 and three captured at Site 8 (Appendix 3, Table A3.1). The tracking data revealed that seven of these fish remained exclusively in the River Bure and associated off-channel habitats for the duration of the tracking period, while one individual occupied the River Ant tributary for 19 % of its time. The scales of isoscape-predicted displacement distance and maximum displacement distance measured by telemetry were significantly positively correlated (R^2 = 0.45, $F_{1,6}$ = 6.77, p = 0.04; Figure 4.5a), with the gradient not significantly different to 1.0 (95 % CI: 0.61 – 1.36), indicating that isotopic data at the time of tagging were a good predictor of the spatial extent of the subsequent movement of individual fish. However, the isotopic data were unable to predict the directionality of displacement (upstream or downstream), as indicated by the relationship being non-significant (R^2 = -0.10, $F_{1,6}$ = 0.38, p = 0.56; Figure 4.5b). Standard linear regressions confirmed there was no relationship between fish length and $\delta^{13}C$, $\delta^{15}N$ or maximum displacement distance recorded by telemetry ($R^2 \leq 0.30$, $F_{1,6} \leq 2.55$, $p \geq 0.16$).

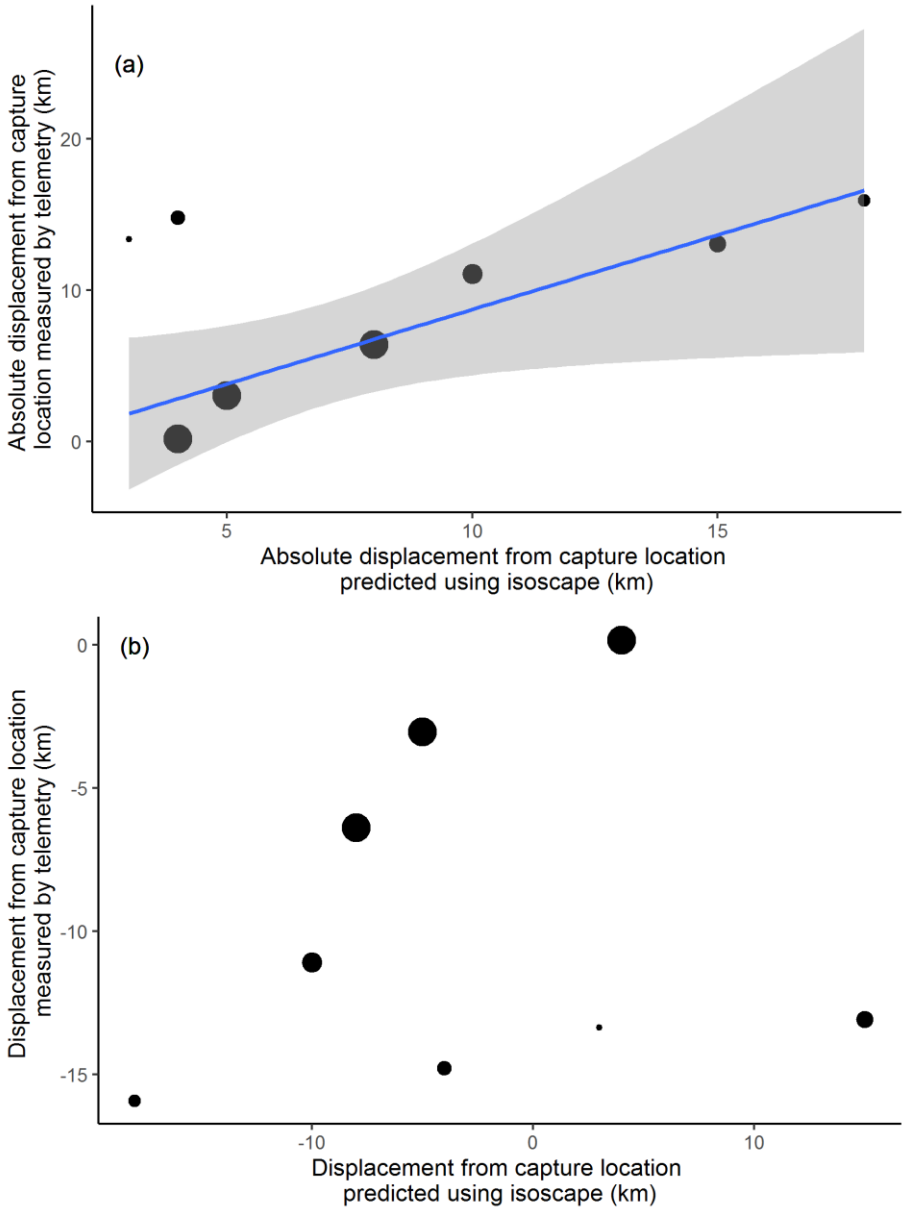

Figure 4.5: Relationship between absolute (a) and directional (b) isoscape-predicted displacement distances and telemetry-observed displacement distances of common bream from capture locations. Data were weighted according to time spent within 8 km of maximum displacement recorded by telemetry, represented by point size.

4.5 Discussion

The study revealed predictable enrichment in $\delta^{13}C$ and $\delta^{15}N$ with distance downstream for both roach and amphipods (a putative food resource of roach) in the study river. This geographic variation in $\delta^{13}C$ and $\delta^{15}N$ was successfully modelled using isoscapes and, subsequently, the dual-isotope assignment procedure of roach was the most reliable in assigning the predicted foraging locations in relatively close proximity to their capture location. The application of this dual isoscape procedure to common bream then demonstrated that the extent of their isotopic disequilibrium with resources at their capture location was a significant predictor of the spatial extent of their subsequent movements.

The lack of an interaction term in either the $\delta^{13}C$ or $\delta^{15}N$ isoscape models indicated the downstream enrichment patterns of amphipods closely matched those of roach, suggesting localised roach foraging behaviour that contrasted to studies on more vagile species (*S. salar*; Rasmussen et al. 2009). Considering the dietary flexibility of roach (Hayden et al. 2014), this also suggested that longitudinal variation in roach $\delta^{13}C$ and $\delta^{15}N$ was a result of isotopic changes in the baseline geochemistry and, thus, in their food resources rather than site-specific differences in prey choice. Isotopic niches of the upper and lower river reaches did not overlap, with Site 3, although situated on the reach boundary, being isotopically similar to the lower reach, likely due to this being the limit of saline influence (Clarke 1990).

The single-isotope ($\delta^{13}C$ only) assignment method was the least effective at assigning roach foraging locations close to capture locations and was likely compromised by a high level of residual variation that, in some locations, was as large as the average difference in $\delta^{13}C$ at the extremities of the study system. Mean foraging displacement predicted by the dual-isotope assignment method (~8 km) was greater than the expected vagility of roach outside of the spawning period and in the absence of in-stream barriers (<5 km; Lucas et al. 1998). For example, in the River Spree, Germany, the wide-range habitat use of roach (based on 90 % of locations determined by radio-tracking) did not exceed 3.8 km (Baade and Fredrich 1998). Nonetheless, such model error can be considered small when the accuracy of

endogenous chemical tracers is usually measured at watershed or geographically regional scales (Brennan and Schindler 2017, Vander Zanden et al. 2018). Ultimately, the spatial resolution of intrinsic markers is dependent on the degree of elemental/ isotopic variation in the environment, which in freshwater varies from distinct ^{87}Sr:^{86}Sr profiles of whole drainage basins encompassing very large spatial areas (e.g. > 10^6 km^2) (Duponchelle et al. 2016) to separate ^{87}Sr:^{86}Sr and $\delta^{15}N$ profiles of tributaries separated by relativly short distances (< 100 km) (Harrington et al. 1998, Kennedy et al. 2005). Indeed, Rasmussen et al. (2009) recorded error of only ~2 km when predicting the scale of *S. salar* movement, due to a steep $\delta^{13}C$ gradient existing across a relatively small study area. Where isotopic gradients are less variable, this study demonstrates that isoscape assignment accuracy can be improved by use of multiple isotopic markers.

The dual-isoscape assignment for common bream predcited the extent of their foraging displacement from capture locations, which was a significant predictor of the scale of their subsequent movements, though not of the directionality of these movements. This suggests a high level of repeatability of bream general activity (functional habitat use, extent of movements) between years and offers complementary information to previous tracking studies on this species, given individual bream have rarely been monitored for more than one year (e.g. Gardner et al. 2013). For species exhibiting predictable unidirectional migrations, such as juvenile anadromous salmonid fishes, the dual isoscape technique thus offers high potential for determining distance travelled. However, for species that are more variable in their use of functional habitats, especially in non-linear, heterogeneous environments, then the method may be less robust in its predictions. Elsewhere, biotelemetry has been used to validate the isoscape tracking of birds and reptiles (Jaeger et al. 2010, Vander Zanden et al. 2015a), but has also highlighted the limitations of isoscape tracking where SI signatures may not be spatially defined (Coffee et al. 2020). Nonetheless, isoscape tracking can be effective in environments with measurable isotopic gradients, even at relatively fine spatial scales, as demonstrated here.

Due to varying rates of isotopic turnover in fish tissues, the isoscape assignment results likely reflect the foraging locations of fish at several weeks or months prior to their capture. Studies have revealed that the SI turnover rate (as its half-life) of fin tissue varies between species, being 13 days in juvenile rainbow trout *Oncorhynchus mykiss* (Heady and Moore 2013), 26 days in juvenile Japanese seabass *Lateolabrax japonicus* (Suzuki et al. 2005), 95 days in juvenile barbel *Barbus barbus* (Busst and Britton 2018) and 133 days in juvenile Colorado pikeminnow *Ptychocheilus lucius* (Franssen et al. 2016). Despite this variability in half-lives between species, these figures suggest that the data in the present study reflect resources accumulated over the summer foraging period that occurred just prior to fish sampling. The use of tissues with more rapid rates of isotopic turnover, such as mucus (Ibarz et al. 2019, Winter et al. 2019), could facilitate isoscape tracking with greater temporal resolution.

In the Bure study system, seasonal variability in isoscapes potentially occurs due to cyclic patterns of algal productivity (Moss and Balls 1989, Torniainen et al. 2017), as well as considerable tidal surges and saline intrusions in winter (Clarke 1990). This is likely to result in a steeper gradient in $\delta^{13}C$ between the upper and lower river reach in winter than was demonstrated here. Moreover, increased winter precipitation and seasonal agricultural practices can also impact isotopic baselines (Finlay and Kendall 2007). Nevertheless, given that the two model species were both cyprinids that rarely grow at temperatures < 12 °C (Britton 2007), their SI data in winter would likely still represent their summer diet (Perga and Gerdeaux 2005), and thus winter-based isoscapes might be less suitable for predicting the extent of their movements. However, seasonal variability in SI data may be more apparent in other species where over-winter growth is more likely to occur, such as in *S. salar* (e.g. Simmons et al. 2020), or in apex predators such as Northern pike *Esox lucius* that can assimilate resources over a longer time period (Vander Zanden et al. 2015b). Should the isoscape tracking technique be applied to other species, then it may be appropriate to combine multiple seasonal isoscapes, where samples of putative food resources are taken for SI analyses at repeated intervals.

For many freshwater systems, downstream hydrological transport is likely to influence the spatial variability of isotopes, for example abrupt changes at tributary junctions or point sources of pollution. Given the tidal nature of the River Bure study system, this was not considered problematic, but elsewhere it may need accounting for in both sample collection and data analyses. Brennan and Schindler (2017) successfully applied a combination of dendritic and traditional Euclidean modelling approaches to strontium isoscapes in a North American river system, to reconstruct the freshwater movement patterns of Chinook salmon, *Oncorhynchus tshawytscha*. This technique may play a significant role in the development of future riverine isoscape applications. Indeed, combining multiple-isotope isoscapes with the dendritic modelling approach offers a novel avenue for further freshwater research.

In summary, this is the first probabilistic assignment to origin for riverine species using dual-isotope isoscapes. The study demonstrated that a dual-isotope assignment procedure is preferential for determining the extent of foraging movements of lowland river fish at moderately fine spatial scales. The increased application of this procedure (over single-isotope tracking) to movement studies is recommended, particularly where telemetry is deemed unsuitable, or can only be applied to limited numbers of animals.

5 Movements of common bream *Abramis brama* in a highly-connected, lowland wetland reveal spatially discrete sub-populations with diverse migration strategies

5.1 Abstract

1. Freshwater ecosystems are increasingly characterised by high levels of fragmentation that restrict the movements of mobile fauna. Yet studies also suggest the migratory behaviours of potamodromous fishes can be highly variable in barrier-free systems, where differing migratory behaviours enable populations to exploit a wide range of food and space resources. This intra-population divergence in spatial and temporal resource use is important to our ecological understanding of distribution patterns and spatial population structure.

2. Common bream *Abramis brama* ('bream') is a potentially strong model species for testing the importance of divergent migration patterns in lowland rivers, but existing studies have been largely restricted to spatially confined and/or anthropogenically-modified systems. This study's principal focus was to examine the diversity of bream migration behaviour in a highly-connected, lowland system using passive acoustic telemetry, which provided continuous, multi-year data on the movements of 181 bream across a tidally-influenced, lowland wetland in eastern England (~60 km of continuous river length plus numerous interconnected shallow lakes and dykes). Tracked bream were grouped according to their initial location and timing of tagging.

3. Bream migratory behaviours varied considerably between tagging groups, but with greater consistency within groups. There was little mixing of groups outside of spawning periods, with season and tidal phase being significant predictors of movements. Rates of movement and swimming speeds were highest in spring, with movements also generally occurring in the direction of tidal flows.

4. For fish tagged just prior to spawning, there was considerable diversity in their post-spawning movements, with some remaining in the immediate vicinity and others that moved to areas ~ 25 km away. These spatially discrete patterns remained until the following spawning period, with high individual consistency in movement behaviour between years.

5. These results suggest this lowland fish population is comprised of several distinct, semi-independent subpopulations that only share space resources in their spawning period. This indicates the importance of connectivity in lowland freshwater systems for enabling and maintaining high phenotypic diversity in the migration behaviours of potamodromous fishes.

5.2 Introduction

Freshwater biodiversity is increasingly imperilled by factors including the destruction or degradation of habitat (Dudgeon et al. 2006, Reid et al. 2019). This includes the loss of longitudinal and lateral riverine connectivity, with few rivers now flowing uninterrupted to sea due to anthropogenic barriers (Grill et al. 2019). In Great Britain, at least 97 % of the river network is impacted by anthropogenic engineering, with even small structures presenting impediments to fish movements (Jones et al. 2019). Yet maintaining longitudinal and lateral connectivity is vital for many riverine fish species to access critical functional habitats for foraging, refugia and spawning (e.g. Lucas et al. 2009, van Puijenbroek et al. 2019). Indeed, river and wetland habitats of high connectivity typically show higher fish abundance and diversity (Fullerton et al. 2010, Nislow et al. 2011), indicating a strong link between connectivity and population- and ecosystem-level processes (e.g. Brodersen et al. 2011).

The impact on fish populations of river fragmentation, movement barriers and subsequent restoration programmes has received considerable research attention in the last decade, especially for diadromous species (e.g. Noonan et al. 2012, Hogg et al. 2015). There has been less focus on non-diadromous fishes, despite some potamodromous species undertaking considerable migrations during their lifecycle

(e.g. Brönmark et al. 2014, Benitez et al. 2018). It is increasingly recognised that highly divergent migration behaviours can exist within populations of potamodromous fauna, allowing these populations to exploit spatially and/ or temporally discrete resources (Kessel et al. 2018). For example, in lake sturgeon *Acipenser fulvescens*, five distinct migration behaviours were detected in the Great Lakes of North America that varied in their phenology and duration of river and lake use (Kessel et al. 2018). Additionally, in populations of the cyprinid fish roach *Rutilus rutilus*, individuals with both fixed (obligate migrant, obligate resident) and flexible migratory strategies are evident, although the genetic and/ or environmental determinants of this plasticity are unclear (Brodersen et al. 2014). Understanding how this intra-population variability in migratory phenotypes can be incorporated into management efforts to conserve and restore freshwater ecology is challenging (Lennox et al. 2019), but studies that explore the range of these divergent movement behaviours in barrier free habitats can inform this process.

The common bream *Abramis brama* ('bream') is a relatively large-bodied cyprinid fish (regularly attaining lengths >500 mm), found abundantly in lowland river systems across Europe and with capacity for partial and facultative migration over distances of at least 60 km (Lucas and Baras 2001). While bream may be more nomadic than other riverine cypriniformes, such as barbel *Barbus barbus* (Schulz and Berg 1987, Brodersen et al. 2019), tracking studies have also suggested that populations demonstrate predictable seasonal habitat shifts and distinct spawning migrations, such as between mainstem and tributary or off-channel habitats (Molls 1999, Lucas and Baras 2001, Skov et al. 2011, Gardner et al. 2013). Notably, spring aggregations of bream may break down into smaller subpopulations with varying migratory tendencies following spawning (Whelan 1983). However, the broader ecological applicability of these tracking studies are potentially limited as they have been constrained to small sample sizes (<10 individuals) and short durations (<1 year), and/or applied in either highly restricted spatial areas (<10 km; Molls 1999, Lyons and Lucas 2002, Skov et al. 2011, Brodersen et al. 2019) or in anthropogenically modified systems that could inhibit the expression of natural behaviours (Gardner et al. 2015a). Thus, while bream have potential as a strong model species for testing the diversity of migratory behaviours within populations of

lowland potamodromous fishes, the extent of their inter-individual variability within highly connected systems has yet to be described.

The aim of this study was to examine the diversity of bream migration behaviours in a highly-connected wetland system in order to understand its influence on their spatial occupancy patterns and population structure. The approach used passive acoustic telemetry to provide continuous, multi-year measurements of the movements of a large sample of adult bream (181 individuals) in the northern Norfolk Broads, an internationally important and protected wetland in eastern England (Natural England 2020). The flooded peat diggings of the Broads National Park were abandoned in the 14th century and, aside from localised biomanipulation projects that restrict fish access in some small areas (e.g. Moss et al. 1996), they have since remained largely free of physical barriers to fish movements. The objectives were to: (1) describe the range of population-scale movements of bream within the River Bure wetland study system; (2) assess the influence of the timing and location of tagging, as well as abiotic factors, on bream movement patterns, including on the extent of their vagility and speed of movement; and (3) determine whether the diversity of migration behaviours in this system suggests the bream population is comprised of several spatially discrete sub-populations.

5.3 Methods

5.3.1 Study area

The focal study area was the River Bure wetland system that forms the northern area of the Broads National Park. This comprises the main River Bure, its two tributaries the Rivers Ant and Thurne, plus numerous interconnected small shallow lakes (medieval peat diggings termed 'broads') and dykes (Figure 5.1). The Bure is 87 km in length, flows south-east towards Breydon Water estuary at Great Yarmouth, and has a mean discharge of 6 $m^3 \cdot s^{-1}$ into the North Sea. The Ant is 27 km in length and the Thurne is 11 km in length. The system is tidal and conductivity (as a measure of salinity) can reach 50,000 $\mu S \cdot cm^{-1}$ at Acle (Figure 5.1), with major saline incursions

often occurring during tidal surges and/ or low river flows that have led to dramatic fish kills (BBC 2014).

The River Bure study system encompassed approximately 60 km of river length (not including lateral connections; Figure 5.1) and was divided into four reaches: Upper Bure, Lower Bure, River Ant and River Thurne. The upper limit of saline incursion on the River Bure (Horning, Figure 5.1; Clarke 1990) provided the boundary between the Upper Bure and the Lower Bure reaches. Outside the urbanised areas of Wroxham and Horning, the Upper Bure reach is predominantly characterised by banks of wet woodland, chiefly alder carr, with small patches of reedbed and a high density of laterally connected broads and dyke systems. This transitions to a semi-artificial landscape of open, reed-fringed grazing marshes in the Lower Bure. The River Ant is similar in character to the Upper Bure reach and features extensive marsh dyke systems, while the River Thurne is more open and includes the largest of the broads (Hickling Broad, 140 ha, Figure 5.1), alongside abundant areas of reedbed. The Thurne is brackish due to underground exchange between the sea and the catchment's groundwater (Pallis 1911) and is at particularly high risk of blooms of *Prymnesium parvum*, an algal species toxic to fish (Holdway et al. 1978), although the reach has the highest abundance and species richness of aquatic macrophytes across the study area (Broads Authority 2019). Channel widths across the upper limits of the study area are approximately 25 m wide with depths to 1.5 m, while in the lower reaches they increase to > 40 m, with depths of over 3 m.

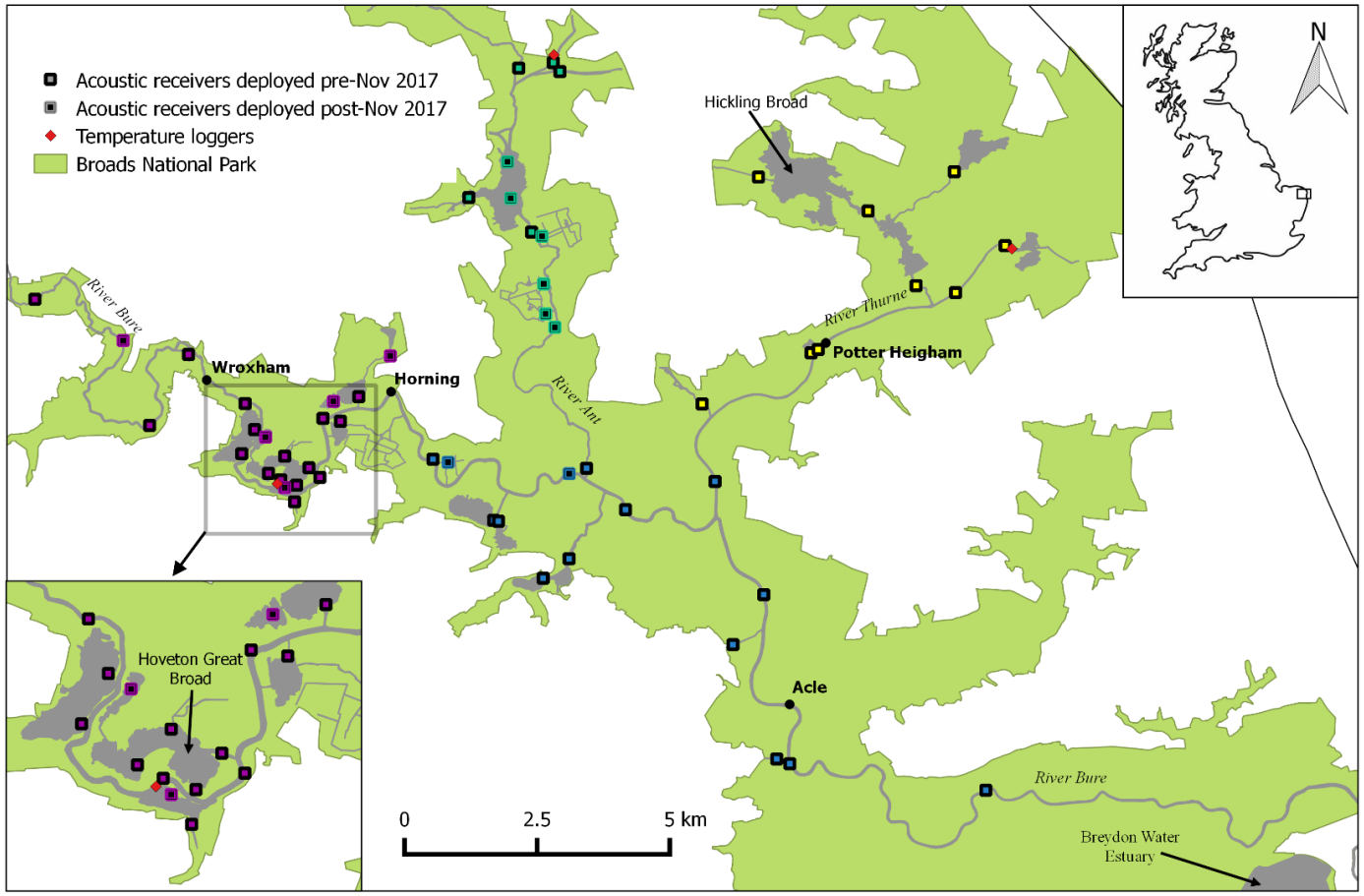

Figure 5.1: Map of the River Bure study system, showing the locations of acoustic receivers according to river reach (Upper Bure = Purple; Lower Bure = Blue; Ant = Green; Thurne = Yellow) and date of deployment. Temperature loggers and points of interest are also shown.

5.3.2 Fish sampling and acoustic telemetry

Fish were captured and tagged between November 2017 and September 2018, resulting in six distinct groups of tagged fish that varied by the date and location of tagging (Table 5.1). Due to the inefficiency of general fish sampling methods (e.g. electric fishing, seine netting, fyke netting) in these large, open waterbodies (Radinger et al. 2019), all fish were captured by rod and line angling. Fish were measured (fork length; ± 1 mm) and, where possible, sexed. Sex was determined by inspecting the shape of the urogenital opening, and for bream sampled in spring, close to their spawning period (UB-2; Table 5.1), by examining their body shape and the presence of spawning tubercles on the head, where the latter indicates a male fish (Poncin et al. 2011). Under general anaesthesia (Tricaine methanesulfonate, MS-222), each fish was then surgically implanted with an internal acoustic transmitter ('tag') sourced from Vemco (V13: length 36 mm × diameter 13 mm, 6.0 g mass in water, N = 148; V9: length 27.5 mm × diameter 9 mm, 2.7 g mass in water, N = 9) or Thelma Biotel (ID-LP13: length 28 mm × diameter 13 mm, 5.5 g mass in water, N = 24). Acoustic tags operated at 69 kHz and pulsed randomly every 60 to 120 s, ensuring that adjacent signals did not continuously overlap and cause interference. Tags were inserted ventrally and anterior to the pelvic fins and incisions were closed with a single suture and wound sealer. Following their return to normal body orientation and swimming behaviour, the fish were released close to their capture location. The movements of the tagged fish were then monitored within an array of receivers for up to two years (to 5 November 2019). All surgical techniques were completed under the UK Home Office project licence 70/8063 and after ethical review.

Table 5.1: Details of common bream sampling locations, tagging dates and acoustic tracking duration by group in the River Bure study system. Length and tracking duration are represented by the range of values, with mean ± SD in parentheses.

Group Name	Sampling location	Tagging date(s)	Length (mm)	Tracking duration (days)	N
UB-1	Upper Bure	6 Nov 2017 – 8 Nov 2017	374 – 491 (435 ± 28)	0 – 725 (217 ± 198)	26
LB-1	Lower Bure	8 Nov 2017 – 9 Nov 2017	286 – 471 (362 ± 70)	25 – 524 (181 ± 173)	8
TH	Thurne	14 Jan 2018	341 – 471 (394 ± 32)	40 – 371 (132 ± 80)	17
AN	Ant	27 Jan 2018 – 29 Jan 2018	362 – 502 (406 ± 34)	28 – 645 (286 ± 235)	25
UB-2	Upper Bure	20 Apr 2018 – 23 Apr 2018	313 – 527 (413 ± 44)	18 – 562 (414 ± 217)	62
LB-2	Lower Bure	15 Sep 2018 – 18 Sep 2018	290 – 503 (389 ± 54)	2 – 414 (177 ± 147)	43

A fixed array of 43 acoustic receivers (Vemco, VR2W) was installed throughout the study system (Figure 5.1) in October 2017, prior to the first fish sampling and tagging event. A further 13 receivers were deployed in January 2018 (N = 1) and in March 2019 (N = 12) to expand the monitored area (Figure 5.1). Receivers situated in the mouths of the Rivers Ant and Thurne tributaries were categorised as 'Lower Bure' due to their proximity to the Lower Bure reach (Figure 5.1). Receivers were placed in the channel margins at approximately mid-water depth. Data were downloaded every three months, while batteries were replaced annually. Detection range was highly variable according to local environmental conditions, but very rarely fell below channel width distance (Chapter 2). Distance measurements between receivers represented the mid-channel circuitous distance.

5.3.3 Environmental data

Water temperature (± 0.5 °C) was recorded at hourly intervals by three data loggers (HOBO® Pendant; model MX2202, Onset Computer Corporation; Figure 5.1). Water temperatures recorded between 9 August 2018 and 7 November 2019 in the River Bure were highly correlated with those in the Rivers Ant and Thurne ($r > 0.99$ and $p < 0.001$ for all pairwise comparisons). Consequently, only River Bure temperature data were used in further analyses. Conductivity and river level data, recorded at 15-min intervals at Acle (Figure 5.1), were sourced from the Environment Agency. These data were offset by 30 minutes to account for the time difference between high tide at Acle and Horning/Potter Heigham (Figure 5.1).

5.3.4 Data and statistical analyses

Movement data were initially explored and visualised using the package *actel* (Flávio 2020) in R 4.0.2 (R Core Team 2020) that enabled calculation of the daily number of bream from each group present in each reach, providing descriptive information on their general movement and reach occupancy patterns. Data collected in the first seven days following tagging were excluded from analyses (in case the fish were demonstrating abnormal behaviours in their immediate post-tagging period), as were data from stationary tags, which occurred due to fish death or tag

expulsion within range of an acoustic receiver. A chi-squared test examined whether overwintering reach occupancy patterns (mean proportion of fish in each reach per day between 1 December and 28 February) differed between groups (when group sample size > 5), where significance values were computed using Monte Carlo simulation with 10,000 replicates. 'Total seasonal range' for each fish in each season was estimated as the distance (in river km) between the furthest upstream and furthest downstream detections, and where this included two or more rivers, the distances were summed. Lateral connections were not included in range estimates.

Continuous-time multistate Markov models (CTMMs) then analysed fish movements between the reaches, using the package *msm* (Jackson 2011). CTMMs assessed the instantaneous rate of transition (i.e. the movement of fish) between discrete spatial states (reaches) in continuous time, whilst allowing for time-constant and time-dependent explanatory variables (Jackson 2011). This relied on the Markov assumption that transition rate was dependent only on the current state and was independent of the movement history of an individual fish or the time it spent in previous states. Correspondingly, the staggered-entry of fish into the study (i.e. the six discrete tagging events) did not require left-censorship (whereby possible spatial states prior to tagging would be accommodated into the model). Fish that were not detected within three months of the study end date were considered deceased or lost from the study (Chapter 3) and entered a 'Lost' absorbing state immediately following their final acoustic detection. While the river reaches represented the discrete spatial states, the Ant and Thurne reaches were combined to aid model convergence. The previous descriptive information on reach occupancy compensated for this loss of accuracy in the model. The resulting states were 'Upper Bure', 'Lower Bure', 'Tributaries' and 'Lost'. The time variable represented the number of days since the start of the study.

The time-constant covariates tested were fish length and sample group, while the time-dependent covariates tested were water temperature, conductivity, river level, tidal phase (high, ebb, low, flood), time of day (day, night), season and year. Sex determination for 11 bream was considered unreliable and univariate CTMMs run on the reduced dataset did not always converge (Appendix 4, Table A4.1), and so the

covariate 'sex' was excluded from this analysis. Detection data for CTMMs were converted into hourly records of fish locations (i.e. states) and combined with the corresponding environmental conditions for each time step (hourly means where necessary). Time of day was classified for each observation according to sunset and sunrise times for the study area, which were extracted from the package *suncalc* (Thieurmel and Elmarhraoui 2019). Season was defined as: spring (1 March to 31 May), summer (1 June to 31 August), autumn (1 September to 30 November) and winter (1 December to 28 February). Covariate effects were explored only for movements between the river reaches and not for transitions between the reaches and the 'Lost' state. Hazard ratios (HR) indicated the strength of covariate effects; HR < 1 indicated a negative effect, HR = 1 was no effect and HR > 1 indicated a positive effect. The effect was considered significant if 95 % confidence intervals did not overlap 1.0, or for categorical covariates, if the CIs did not overlap each other.

The mean residency in each reach, plus the expected number of visits to each reach prior to transition into the 'Lost' state, were calculated from the best-fitting CTMM. Selection of the best-fitting model followed the minimisation of Akaike information criterion values (AIC), with models exhibiting $\Delta AIC \leq 2$ also awarded strong support, provided they were parsimonious (Burnham and Anderson 2002, Richards et al. 2011). Initially, covariates were parameterised separately in univariate models, with those resulting in reduced AIC compared in multivariate models. Models containing both fish length and sample group as covariates were disregarded due to length differing significantly by group (ANOVA: $F_{5,175} = 5.71$, $p < 0.001$). Similarly, a significant relationship between some environmental variables and seasonality meant they were not modelled together (Time of day ~ season, $\chi^2_{(3,\ 17496)} = 883$, $p < 0.001$; ANOVA: Temperature ~ season, $F_{3,17492} = 17{,}123$, $p < 0.001$; Conductivity ~ season, $F_{3,17492} = 659$, $p < 0.001$; River level ~ season, $F_{3,17492} = 1002$, $p < 0.001$). Where interdependencies arose, only the covariates resulting in the greatest reduction in AIC were retained for further comparison in multivariate models (Table 5.2).

The package *actel* (Flávio 2020) also facilitated examination of the speed of movement for fish moving between reaches. Generalised additive mixed models

(GAMMs) were applied to testing the effect of fish length, sex, sample group, day of year (DOY; Julian day, representing seasonality), year and route (i.e. between which reaches, irrespective of direction) on the speed of movement using the *gamm4* package (Wood and Scheipl 2020). This was performed through the uGamm wrapper function from the package *MuMIn* (Barton 2020) to allow automatic multi-model inference based on corrected AIC (AICc) values. The data required a Gaussian family structure and identity link function, with a random effect of fish ID accounting for between-individual variation. A non-linear effect of DOY was modelled using a cyclic cubic regression spline as a smoothing function. The degrees of freedom of the smooth term were limited to a maximum of 3 to avoid overfitting. As above, fish length and sample group were not modelled together. GAMMs incorporating and comparing the effects of fish sex were performed on reduced datasets due to missing data (as described above). Analysis of residual plots ensured model adequacy.

Table 5.2: The combinations of covariates tested in CTMM models that examined rate of movement of common bream between reaches in the River Bure study system. Models are ordered by Akaike Information Criterion (AIC) values.

Model	ΔAIC
~ Group + Season + Tidal phase + Year	0.00
~ Group + Season + Tidal phase	25.51
~ Group + Season + Year	27.00
~ Group + Season	52.52
~ Group + Tidal phase + Year	250.75
~ Group + Tidal phase	255.95
~ Group + Year	277.74
~ Group	282.76
~ Season + Year + Tidal phase	442.56
~ Season + Year	469.47
~ Fish Length*	472.27
~ Season + Tidal phase	476.25
~ Season	502.96
~ Light*	690.99
~ Tidal phase + Year	699.92
~ Temperature*	700.93
~ Tidal phase	710.70
~ Conductivity*	711.02
~ Year	726.80
~ River level*	727.77
~ Null	737.63

*Covariates not compared in multivariate models due to interdependency with another covariate exhibiting higher explanatory power

5.4 Results

5.4.1 Spatial occupancy by sampling group and river reach

The 181 tagged bream were tracked for between 0 and 725 days (Table 5.1). Eight fish were removed from all analyses due to tracking durations of less than seven days, while a further 116 fish transitioned to the 'Lost' state during the study period due to factors including mortality and emigration from the study area (Chapter 3). The remaining 57 fish were all detected within three months of the study end-date. Bream were recorded at 53 of the 56 acoustic receivers in the study area, including all receivers placed in the mainstem Bure, Ant and Thurne across approximately 60 km of river length (Figure 5.1). Total seasonal range of individuals varied from 0 (detected at only one receiver) to 26.7 km, with ranges generally expanding during spring and contracting during summer (Figure 5.2).

Bream from groups UB-1 and AN remained predominantly in their respective sampling reaches throughout the study and none of these fish were ever recorded in the River Thurne (Figure 5.3). LB-1 and LB-2 bream had similar reach occupancy profiles, with the highest daily abundance in the Lower Bure reach, but with some overwintering presence in the River Thurne, and to a lesser extent the River Ant (Figure 5.3). TH bream showed high fidelity to the River Thurne in summer and winter, but not in their spring spawning period when they moved mainly into the Upper Bure reach (Figure 5.3). This pattern was similar in a subset of UB-2 fish (24 %); whilst they had been tagged in the Upper Bure in spring, they were then largely resident in the Thurne during summer and winter (Figure 5.3). However, a large proportion of UB-2 fish (47 %) remained resident in the Upper Bure throughout the study period, with the remaining proportion (29 %) utilising the Lower Bure at various times of the year (Figure 5.3). No fish from groups TH or UB-2 entered the River Ant during the study period. Overwintering reach occupancy differed significantly between the sampling groups ($\chi^2 = 1180.3$, $p < 0.001$), with most fish (63-100 %) remaining within the reaches in which they were tagged. Furthermore, the reach occupancy profiles revealed almost no active fish from any of the groups were present in the River Thurne during the period of peak spawning activity.

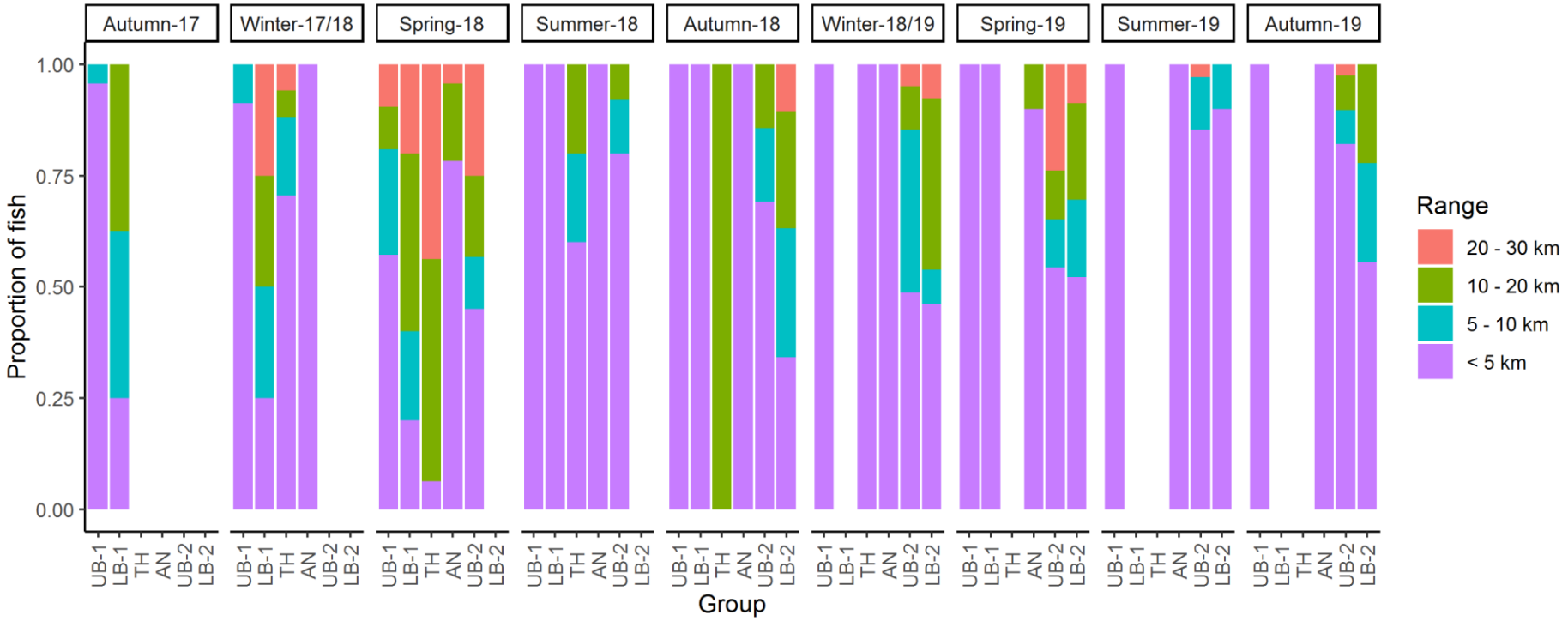

Figure 5.2: Total seasonal range of common bream in the River Bure study system, expressed as the proportion of fish in each group and season for each set of values.

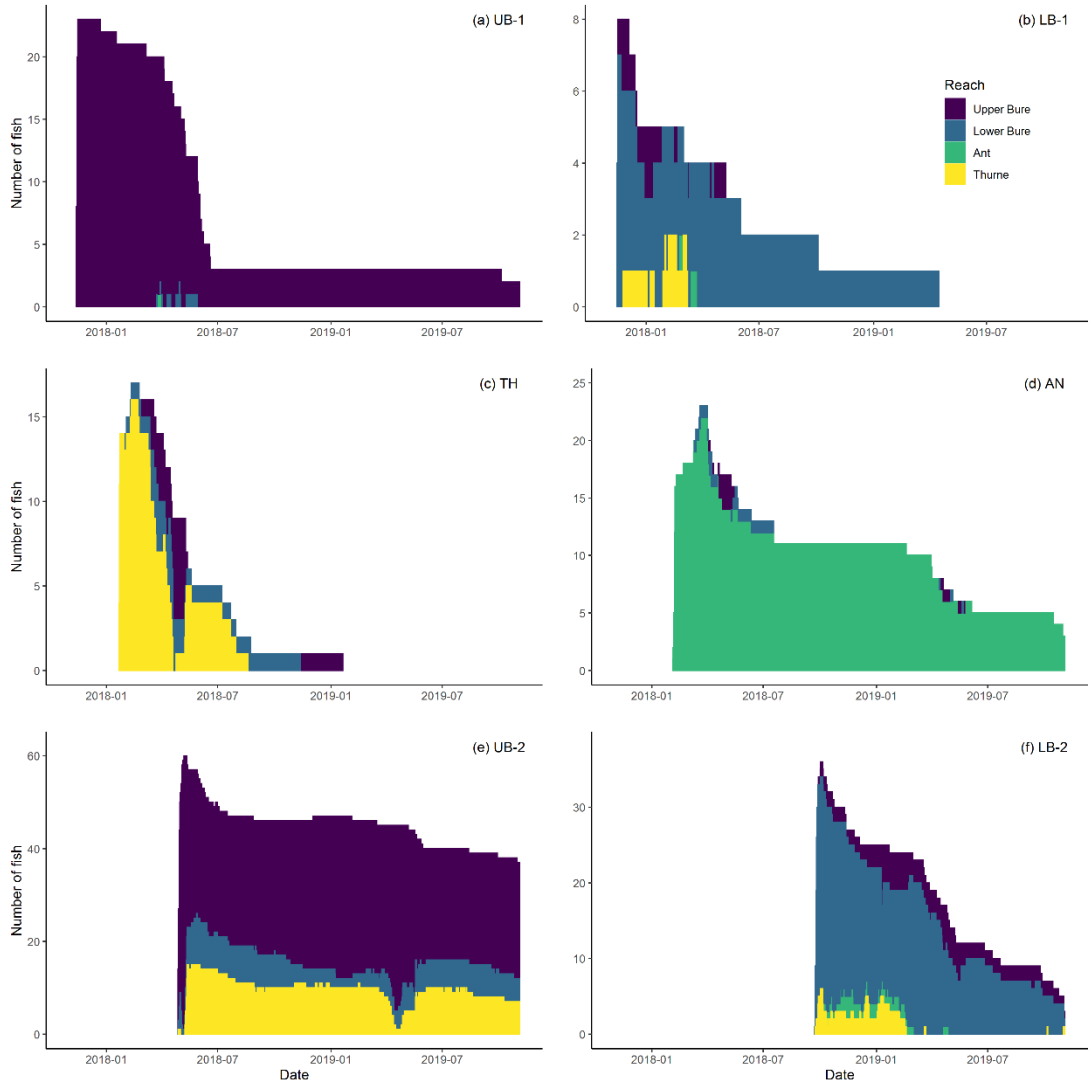

Figure 5.3: Occupancy profiles of common bream in the reaches of the River Bure study system according to tagging group.

5.4.2 Continuous-time multistate Markov modelling of movement rates

The best-fitting CTMM describing the movements of bream between reaches retained tagging group, season, tidal phase and year as explanatory variables (Tables 2, 3, 4). No other combinations of covariates had strong support under the selection criteria.

The effect of group revealed that bream in UB-1 and UB-2 had the lowest rates of transition from the Upper Bure to Lower Bure, while bream in LB-1 and LB-2 had the highest (Table 5.3). For movements from the Lower to Upper Bure, fish in UB-1 transitioned at a significantly higher rate than LB-1 and LB-2, suggesting fish tended to move more readily towards their tagging locations. The rate of upstream movement from the Lower Bure into the Tributaries was not significantly affected by group, although AN fish had a lower rate of downstream movement from the Tributaries into the Lower Bure than bream from UB-1 and LB-1 (Table 5.3). For the effect of season, transition rates between all reaches and in all directions were significantly higher in spring than in all other seasons, except for movements from the Lower Bure into the Tributaries, which occurred at a significantly higher rate during winter (Table 5.3). In addition, upstream and downstream movements between the Upper and Lower Bure were significantly more frequent during winter than during summer.

The effect of tidal cycle revealed that downstream movements of fish from the Upper to the Lower Bure occurred at a significantly higher rate when the tide was receding, while the rate of upstream movement from the Lower Bure into the Tributaries was significantly greater during an incoming tide. Furthermore, a high tide increased the rate of upstream movement from the Lower to the Upper Bure but decreased the rate of downstream movement from the Tributaries to the Lower Bure. The second year of study was associated with a ~60 % reduction in the rates of downstream movement between the Upper and Lower Bure, and upstream movement between the Lower Bure and Tributaries.

5.4.3 Residency, number of visits per reach and speed of movement

For all groups except UB-2, tagged bream were predicted to spend the longest time in their respective sampling reaches, with this particularly evident for groups UB-1 and AN, where average residency exceeded 150 days (Table 5.4). On average, UB-2 fish spent a similar amount of time in the Upper Bure and Tributaries reaches, which reflects the partially migratory nature of this group. Across the groups sampled outside the Upper Bure, TH spent the longest in the Upper Bure (20 days), but this was only significantly different to LB-2. Bream from UB-1 and AN had fewer visits to each reach than bream in UB-2, LB-1, LB-2 and TH, indicating lower levels of migratory activity (Table 5.4).

The best-fitting model predicting speed of movement between reaches retained an effect of route as well as a nonlinear effect of day of year (DOY) (Table 5.5; Figure 5.4). Bream travelled significantly faster (by 0.10 - 0.13 ms^{-1}) when moving between the Thurne and Lower Bure reaches than between the Upper and Lower Bure or between the Ant and Lower Bure. In addition, speed of movement peaked during spring at Day 115 (25 April). A random effect of fish ID accounted for 39 % of the residual variation. No other combinations of covariates were retained under the selection criteria.

Table 5.3: Hazard ratio (HR) estimates from the best-fitting Continuous-Time Multi-state Markov models, indicating the covariate effects on the transition rates of common bream between reaches in the River Bure study system. Effects are compared to baseline covariate values (Group = UB-1; Season = Spring; Tidal phase = Ebb; Year = Year 1). 95 % confidence intervals are in parentheses and significant effects are in bold.

		Movement / Transition:			
Covariate		Upper Bure > Lower Bure	Lower Bure > Upper Bure	Lower Bure > Tributaries	Tributaries > Lower Bure
Group:	UB-2	**7.44 (3.16, 17.51)**	0.58 (0.20, 1.70)	2.45 (0.33, 18.19)	0.19 (0.02, 1.74)
	LB-1	**50.95 (17.13, 151.56)**	**0.14 (0.04, 0.48)**	0.64 (0.08, 4.89)	2.64 (0.28, 24.54)
	LB-2	**51.36 (19.65, 134.21)**	**0.16 (0.05, 0.49)**	0.90 (0.12, 6.81)	1.50 (0.16, 14.28)
	TH	**14.05 (5.10, 38.66)**	0.47 (0.15, 1.49)	2.27 (0.30, 17.09)	0.25 (0.03, 2.27)
	AN	**34.61 (11.60, 103.29)**	1.22 (0.37, 4.11)	4.54 (0.57, 36.36)	**0.02 (0.002, 0.22)**
Season:	Summer	**0.06 (0.02, 0.15)**	**0.07 (0.03, 0.16)**	**0.23 (0.13, 0.39)**	**0.42 (0.24, 0.73)**
	Autumn	**0.18 (0.10, 0.32)**	**0.35 (0.22, 0.56)**	**0.40 (0.25, 0.65)**	**0.28 (0.16, 0.49)**
	Winter	**0.29 (0.17, 0.50)**	**0.53 (0.31, 0.91)**	**2.38 (1.58, 3.60)**	**0.49 (0.32, 0.76)**
Tidal phase:	Flood	**0.55 (0.37, 0.81)**	1.20 (0.79, 1.81)	**1.88 (1.35, 2.62)**	0.71 (0.50, 1.01)
	High	0.65 (0.33, 1.30)	**2.79 (1.67, 4.64)**	1.10 (0.58, 2.09)	**0.40 (0.18, 0.93)**
	Low	**0.43 (0.19, 0.99)**	1.64 (0.88, 3.03)	1.00 (0.51, 1.95)	1.02 (0.59, 1.76)
Year:	Year 2	**0.40 (0.25, 0.62)**	0.85 (0.54, 1.34)	**0.41 (0.26, 0.63)**	1.10 (0.68, 1.77)

Table 5.4: Metrics calculated from the best-fitting Continuous-Time Multi-state Markov model, showing mean residency of common bream and the expected number of visits to each river reach in the River Bure study system prior to a fish transitioning into the 'Lost' state. 95 % confidence intervals are in parentheses. Estimates are presented for different values of the covariate 'Group' (with tagging location in parentheses), while other covariate values were set to zero.

	Group	Reach		
		Upper Bure	Lower Bure	Tributaries (Ant / Thurne)
Mean residency (days):	UB-1	198.12 (112.43 - 349.13)	10.87 (4.53 - 26.04)	7.99 (0.96 - 66.12)
	LB-1	5.62 (2.56 - 12.37)	41.20 (27.36 - 62.04)	3.08 (1.77 - 5.34)
	TH	19.94 (10.78 - 36.85)	13.17 (8.91 - 19.46)	29.66 (19.64 - 44.80)
	AN	8.25 (3.91 - 17.37)	5.90 (3.56 - 9.80)	168.60 (118.13 - 240.65)
	UB-2	36.63 (25.83 - 51.93)	11.49 (8.32 - 15.88)	38.22 (23.92 - 61.09)
	LB-2	5.58 (3.13 - 9.97)	33.45 (23.06 - 48.52)	5.36 (2.87 – 10.00)
Expected number of visits:	UB-1	1.87	2.41	0.45
	LB-1	2.93	7.14	3.27
	TH	4.08	9.27	4.80
	AN	1.86	3.61	1.67
	UB-2	3.62	7.63	3.74
	LB-2	3.14	8.38	4.35

Table 5.5: Results of the best-fitting Generalised Additive Mixed Model predicting the speed of movement of common bream between the reaches of the River Bure study system. The Upper Bure – Lower Bure route is represented by the intercept. Error margins are SE.

	Estimate coef	t value	*P*	Estimate df	F value	*P*
(Intercept)	0.227 ± 0.012	18.73	< 0.001			
Route: Ant – Lower Bure	-0.036 ± 0.031	-1.16	0.25			
Route: Thurne – Lower Bure	0.097 ± 0.015	6.51	< 0.001			
s(DOY)				1.81	555.9	< 0.001

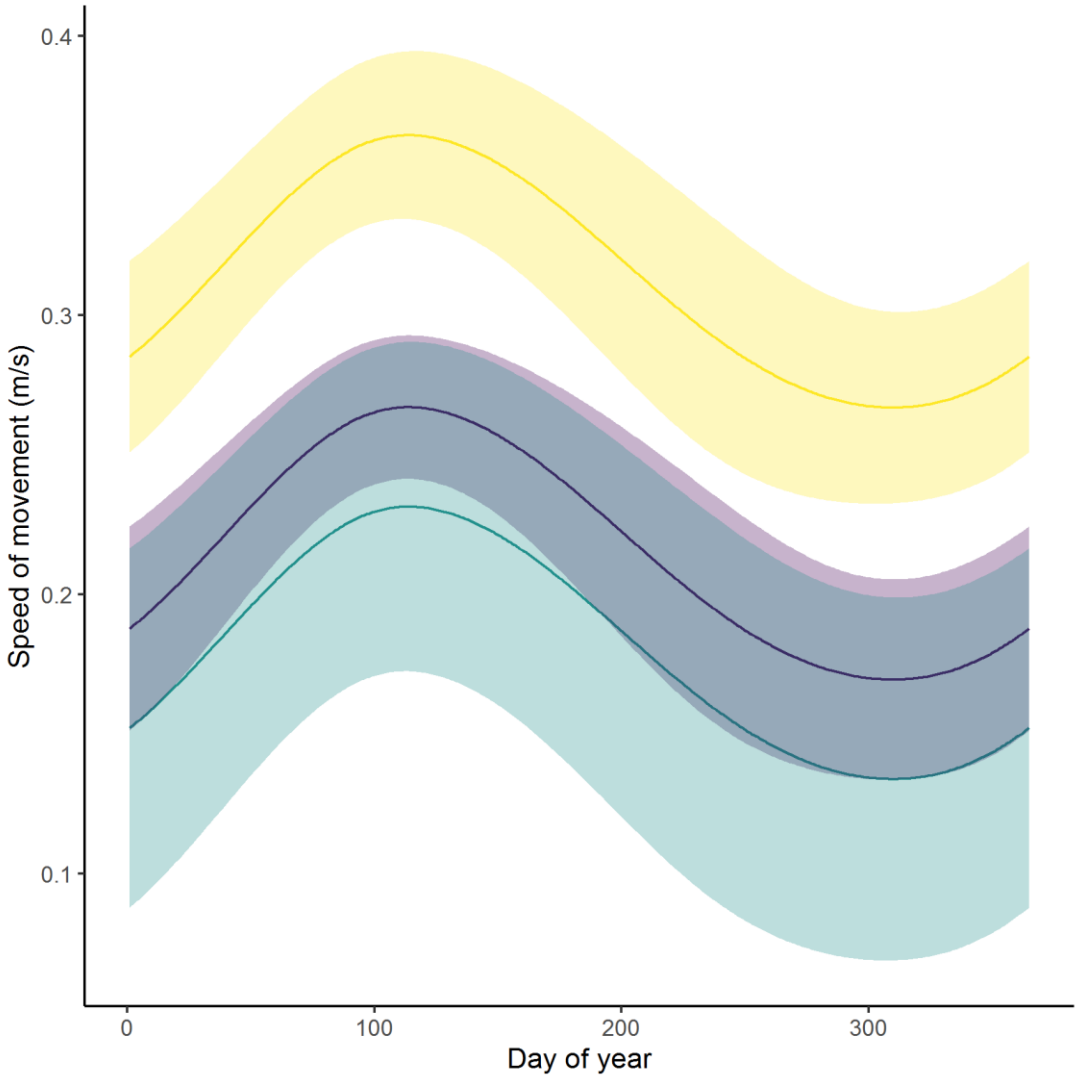

Figure 5.4: Predicted speed of movement of common bream between reaches of the River Bure study system as a function of day of year (Julian day) and travel route (purple = Upper Bure – Lower Bure; blue = Ant – Lower Bure; yellow = Thurne – Lower Bure) according to the best-fitting GAMM. Shaded areas represent 95% confidence intervals. Random effect uncertainty is not accounted for.

5.5 Discussion

Acoustic telemetry revealed the movement behaviour of bream in this highly connected wetland system varied considerably between the tagging groups, but was largely consistent within them, except for the fish tagged just prior to their spawning period. For fish tagged close to the spawning period, their movement behaviours were more divergent, comprising of both year-round Upper Bure residents and migrants that predominantly resided in the River Thurne, approximately 25 km away. These divergent patterns in movements and spatial occupancy were consistent across the study period, with high individual repeatability between the first and second year of study. Thus, these results suggest the bream population comprised several semi-independent subpopulations that resided in spatially distinct areas outside of the spawning period. Furthermore, bream tagged in the River Ant appeared to be reproductively isolated, with limited exchanges of fish between this reach and the rest of the system, including during the spawning period.

There is increasing evidence from multiple taxa (e.g. birds, mammals, fishes) that divergent migration strategies are an important form of life-history diversity that should be considered within management and conservation initiatives (e.g. Gilroy et al. 2016, Tucker et al. 2018, Thompson et al. 2019). In their entirety, these studies suggest that populations of species can no longer be considered as showing one common behavioural pattern but instead comprise groups of individuals that specialise according to their spatial use of the wider habitat. Across the River Bure study system, brackish areas could be providing differential feeding opportunities for adult bream (Kafemann et al. 2000), resulting in spatial differences in bream foraging areas. The migration of some adults between these areas and lower salinity reaches likely reduces the population's dependence on more confined spawning/ rearing habitats and stabilises the population through diversifying space and resource use. This could be increasingly important in future, given the study area is already subject to episodes of saline intrusion that are likely to intensify with sea level rise due to climate change, coupled with blooms of toxic *Prymnesium parvum* that lead to fish mortalities (e.g. Holdway et al. 1978, BBC 2014). The system also faces some loss of connectivity in upper reaches in the near future (planned installation of fish

barriers at Hoveton Great Broad, Figure 5.1, Environment Agency 2020a). As such, there is a management requirement to identify how the expression of this phenotypic - and potentially genetic - variation within the bream population can be maintained in both the immediate and long-term future, given that this species supports a nationally important recreational fishery, while the connectivity of the system is important for the functionality of the ecosystem more widely (Thompson et al. 2019, Blanchet et al. 2020).

This study's large sample size and continuous tracking for two years revealed both known and undescribed movement behaviours in bream. The results support the finding of Whelan (1983), who described divergent migration in bream in Ireland, where fish aggregated during spawning, before subsequently dispersing into smaller groups with differing migratory tendencies. Partial migration of bream into brackish environments has also been inferred through otolith isotopic chemistry (Kafemann et al. 2000). The rate of movement between river reaches was highly dependent on tagging group, which may be explained by the shoaling nature of the species, as opposed to more solitary fishes that exhibit independent divergent migration, such as the lake sturgeon *A. fulvescens* (Kessel et al. 2018). Seasonality was also important for both rate and speed of movement, which builds on work by Gardner et al. (2013) that identified predictable seasonal shifts of adult bream between mainstem and tributary habitats. The novel finding of a significant effect of tidal phase on movement indicated a tendency for bream to exploit natural flow variations for passive transport, most likely to minimise the energetic costs of largescale movements (Taylor and Cooke 2012). Elsewhere, flooding tides have been linked to increased feeding activity of bream in intertidal habitat (Le Pichon et al. 2017), but it remains unclear whether faster movement between the Thurne and Lower Bure reaches is the result of greater tidal flow in this area or simply represents elevated swimming speeds.

The study was effective in demonstrating phenotypic diversity in the movement patterns of bream in this system, with some species making relatively large movements in spring to access spawning grounds, while others were more limited in the extent of their movements. In respect of this diversity, the reliance on angling as

a capture method for the tagged fish could have potentially biased for the selection of specific behavioural phenotypes that are more susceptible to angler capture (Diaz Pauli et al. 2015). For example, resident fish can have increased spatial encounters with anglers that can increase their vulnerability to capture (Alós et al. 2012). However, responses may be species- and population-specific, for example, studies on bluegill *Lepomis macrochirus* report conflicting results regarding susceptibility of both shy and sociable fish to angling (Wilson et al. 2011, Louison et al. 2018). Moreover, the results here revealed both low and high vagility of individuals, suggesting the tagged fish represented a range of phenotypes that were independent of the sampling method. A minimum fish size constraint for acoustic tagging could have also masked an effect of size on rate of movement. Indeed, in small lake systems, the partial migration of bream into overwintering habitats has been associated with size and predation risk (Skov et al. 2011), and the Norfolk Broads' small dyke systems are typically dominated by juvenile and small-bodied cyprinid fishes (Tomlinson et al. 2010). However, documenting these small-scale movements to/ from open water habitats was not the focus of this study. Finally, while it was shown that some bream that were tagged in the River Thurne and Lower Bure moved into the Upper Bure during their spawning period, it is not currently clear whether these groups of fish then mixed on spawning grounds. As such, the extent of gene flow between these sub-populations is currently unknown but represents an important next step to determine.

Phenotypic variation is key to maintaining species' adaptive potential in spatially and temporally heterogeneous environments, and may have already been lost from isolated fish populations in fragmented river systems (Thompson et al. 2019). Furthermore, the suppression of intraspecific diversity through human disturbance potentially decreases the resilience of species to natural and anthropogenic threats, and should not be overlooked regarding models of environmental change (Schindler et al. 2010, Blanchet et al. 2020). The high connectivity of the River Bure wetland system appears to have encouraged the use of a wide range of spatial resources within the bream population and has resulted in the formation of a series of spatially distinct sub-populations across the wider system. These results emphasise the importance of lateral and longitudinal connectivity, and habitat heterogeneity for the

expression of behavioural variability with respect to space and resource use in potamodromous fishes. They can be used to inform the future management of fish populations, including conserving the phenotypic diversity of migratory behaviours in connected systems, and assisting the restoration of suppressed populations in more fragmented systems.

6 Acoustic telemetry reveals strong spatial preferences and mixing during successive spawning periods in a partially migratory common bream population

6.1 Abstract

Partial migration, whereby a population comprises multiple behavioural phenotypes that each have varying tendencies to migrate, is common among many animals. Determining the mechanisms by which these phenotypes are maintained is important for understanding their roles in population structure and stability. The aim here was to test for the temporal and spatial consistency of migratory phenotypes in a common bream *Abramis brama* ('bream') population, and then determine their social preferences and extent of mixing across three successive annual spawning periods. The study applied passive acoustic telemetry to track the movements of bream in the River Bure system of the Norfolk Broads, a lowland wetland comprising highly connected riverine and lacustrine habitats. Analyses revealed that individual migratory phenotype was highly consistent across the three years, but this was not predicted by fish sex or length at tagging. During the annual spawning periods, network analyses identified off-channel areas visited by both resident and migrant fish that, in non-spawning periods, were relatively independent in their space use. Within these sites, the co-occurrence of bream was non-random, with individuals forming more preferred and avoided associations than expected by chance. These associations were not strongly predicted by similarity in fish length, sex or behavioural phenotype, indicating that the resident and migrant phenotypes mixed during their annual spawning periods. The results suggested these different phenotypes, with spatially distinct resource use in non-spawning periods, comprised a single metapopulation, with this having important implications for the management of this wetland resource.

6.2 Introduction

Migration is a diverse phenomenon that exists across taxa and has a strong influence on ecological and evolutionary processes that range from individual levels up to whole ecosystem dynamics (Dingle 1996, Chapman et al. 2012a). Within species,

movement strategies can vary between individuals, with only a proportion of a population being migratory. This is termed 'partial migration' and is widely documented in fishes at a variety of spatial scales (Chapman et al. 2012a), from small potamodromous habitat shifts (< 5 km; Brodersen et al. 2014) to large diadromous and marine migrations (100s to 1000s km; Robichaud and Rose 2004, Augspurger et al. 2017, Ferguson et al. 2019). Understanding partial migration and its role in processes such as gene flow and adaptation is important for monitoring population stability and the conservation and management of species (Chapman et al. 2012a, Turbek et al. 2018).

Reproductive isolation is one mechanism by which the coexistence of sympatric phenotypes can be maintained within a population (e.g. Grabowski et al. 2011, Whitlock et al. 2018, Garduno-Paz et al. 2020). This may occur spatially with, for example, the segregation by depth of different migratory phenotypes of Atlantic cod *Gardus morhua* that utilise the same spawning areas (Grabowski et al. 2011). Isolation can also be temporal, such as through the separation of the early and late spawning runs of kokanee salmon *Oncorhynchus nerka* (Whitlock et al. 2018). Spawning segregation can imply a strong heritability of migratory phenotypes, as observed in some salmonid fishes (Berejikian et al. 2014, Debes et al. 2020), and could preclude population divergence and speciation (Turbek et al. 2018). However, residency and migration are not always genetically differentiated (Adams et al. 2016) and in some populations, each behavioural type may give rise to the other (e.g. Hodge et al. 2016). Alternatively, factors such as body size, inter- and intrapopulation density, predation risk, temperature and/ or resource availability may influence whether an individual fish undertakes a migration (Brodersen et al. 2011, Skov et al. 2011, Montorio et al. 2018). Across multiple years, this decision can depend on prevailing conditions, although in the cyprinid fish roach *Rutilus rutilus,* overwintering migratory strategy was largely consistent within individuals (Brodersen et al. 2014). The partial migration of this species has been intensely studied, but for other non-salmonid, potamodromous species, its prevalence and drivers remain largely unexplored (Chapman et al. 2012b). This is despite evidence of widespread ecological implications from fluctuating levels of fish movement,

such as both bottom-up and top-down effects on trophic dynamics (Brodersen et al. 2011, Hansen et al. 2019b).

The common bream *Abramis brama* ('bream') is a relatively large-bodied cyprinid fish that can exhibit partial migration (Whelan 1983, Skov et al. 2011, Brodersen et al. 2019). Within populations, the propensity to migrate has been linked to size and predation risk, with smaller individuals more likely to seek refuge overwinter in shallow stream habitats (Skov et al. 2011). Elsewhere, in systems comprised of interconnected lakes, their partial nomadic movement has been associated with poor somatic condition (Brodersen et al. 2019). This suggests that populations in separate lakes should be managed as one overall unit or metapopulation, especially given that bream are important ecosystem engineers that can affect ecological stability (Brodersen et al. 2019). This has potentially important implications for the management of wetland systems, including for nutrient dynamics and controlling eutrophication (Phillips and Jackson 1990). With seasonal bream migrations also being important for successful reproduction (Schulz and Berg 1987), then understanding the temporal and spatial use of different lake habitats at key periods of the year, such as the reproductive season, is important.

The Norfolk Broads is a protected wetland of high connectivity in eastern England (Natural England 2020), where preliminary data has suggested the bream population comprises diverse migratory phenotypes (including residents and migrants) that form spatially distinct sub-populations in non-reproductive periods (the authors, unpublished data). While some of these sub-populations then make considerable migrations during their reproductive period, the extent of their spatial and social mixing during spawning remains unclear. This is a critical knowledge gap, as reproductive segregation could suggest that complex genetic processes drive their migratory behaviours and potentially indicate sub-population genetic divergence (Jorgensen et al. 2010, Baerwald et al. 2016). Consequently, through the application of passive acoustic telemetry across three spawning periods, the aim was to investigate the temporal and spatial consistency of migratory phenotypes in the bream population and identify the extent of their reproductive mixing. Accordingly, the objectives were to: (1) evaluate individual consistency in migration strategy

(resident/ migrant) and examine the influence of length and sex on movement type; (2) assess the spatial preferences of bream in their reproductive period (as 'hotspots' of bream detection across the acoustic receiver network); and (3) evaluate the social preferences of bream in their reproductive period, identifying whether their similarity in length, sex or movement type influenced their probability of interaction in time and space.

6.3 Material and Methods

6.3.1 Study area

The study system was the northern area of the Broads National Park, a lowland wetland in eastern England comprised of the main River Bure, its two tributaries the Rivers Ant and Thurne, plus numerous interconnected dykes and small shallow interconnected lakes (medieval peat diggings termed 'broads') (Figure 6.1a). The River Bure is 87 km in length, flows south-east towards Breydon Water estuary at Great Yarmouth, and has a mean discharge of 6 $m^3 \cdot s^{-1}$ into the North Sea. The Rivers Ant and Thurne are 27 km and 11 km in length, respectively. The study area encompassed approximately 60 km of river length (not including lateral connections; Figure 6.1a), with channel widths of 25 to 40 m and depths of 1.5 to 3.0 m. The system is tidal, with the upper limit of saline incursion providing the boundary between the Upper Bure and Lower Bure reaches (at Horning; Figure 6.1a; Clarke 1990). In addition, the Thurne is brackish due to underground exchange between the sea and the catchment's groundwater (Pallis 1911).

Between the urban centres of Wroxham and Horning (Figure 6.1b), river banks are characterised by wet woodland, chiefly alder carr, with small patches of reedbed and a high density of laterally connected broads and dyke systems. This 'Wroxham-Horning' section of the Upper Bure reach has been identified as important for overall fish population density as well as bream spawning, based on the availability of suitable macrophyte substrate within off-channel refugia (Hindes 2019), high abundance of adult fish during spawning periods and high egg densities (Environment Agency, unpublished data). Furthermore, bream spawning migrations

of up to 25 km have been documented from the Rivers Thurne and Ant to Hoveton Great Broad (HGB: Figure 6.1b) and the surrounding area (Chapter 5). Consequently, analyses were largely focused on the movements of bream within the Wroxham-Horning section during their reproductive period.

6.3.2 Fish sampling and acoustic telemetry

A total of 181 bream were captured and tagged between November 2017 and September 2018 across four reaches of the study system; Upper Bure, Lower Bure, Thurne and Ant (Figure 6.1a; Table 6.1). All fish were captured by rod and line angling, as more general fish sampling methods (e.g. fyke netting, seine netting, electric fishing) were too inefficient in such large, open waterbodies (Radinger et al. 2019). Bream were measured (fork length; ± 1 mm) and, where possible, sexed. Sex was determined by inspecting characteristics of the fish, such as the shape of the urogenital opening, and for those sampled in spring, close to their spawning period (Table 6.1), their body shape and secondary sexual characteristics such as the presence of spawning tubercles on the head, where the latter indicates a male fish (Poncin et al. 2011).

Acoustic transmitters ('tags') were sourced from Vemco (V13: length 36 mm × diameter 13 mm, 6.0 g mass in water, N = 148; V9: length 27.5 mm × diameter 9 mm, 2.7 g mass in water, N = 9) and Thelma Biotel (ID-LP13: length 28 mm × diameter 13 mm, 5.5 g mass in water, N = 24). Tags operated at 69 kHz, with battery lives of between 29 and 46 months, and with random transmission intervals between 60 and 120 s ensuring that adjacent signals did not continuously overlap and cause interference. Tags were surgically implanted into the ventral body cavity of the fish, anterior to the pelvic fins and incisions were closed with a single suture and wound sealer. All regulated procedures were performed with the fish under general anaesthesia (Tricaine methanesulfonate, MS-222), following ethical review and under the UK Home Office project licence 70/8063. Fish were released close to their capture location following their return to normal body orientation and swimming behaviour. Their movements were then monitored within an array of receivers for up

to ~2.5 years (to 30 June 2020), encompassing three reproductive periods in the years 2018-2020.

A fixed array of 44 acoustic receivers (Vemco, VR2W) was installed in October 2017 and January 2018 throughout the four reaches of the study system (Figure 6.1a), prior to the first bream reproductive period in spring 2018. A further 12 receivers were deployed in March 2019 to expand the monitored area (Figure 6.1a). Receivers were mostly moored on posts or underwater structures and placed in the channel margins at approximately mid-water depth. Data were downloaded every three months, while batteries were replaced annually. Receiver detection range varied with local environmental conditions, but rarely fell below channel width distance (Chapter 2).

6.3.3 Environmental data

Water temperature (± 0.5°C) was recorded at hourly intervals by two data loggers in the Rivers Bure and Ant (HOBO® Pendant; model MX2202, Onset Computer Corporation; Figure 6.1a). A linear regression model revealed that temperature in the River Ant was a highly significant predictor of temperature in the River Bure ($F_{1,5733}$ = 776,600, $p < 0.001$, R^2 = 0.99). Analyses principally used temperature data from the River Bure, however where this was unavailable (post November 2019), River Bure temperature was estimated according to the linear equation: $Bure = (0.99 \times Ant) - 0.21$.

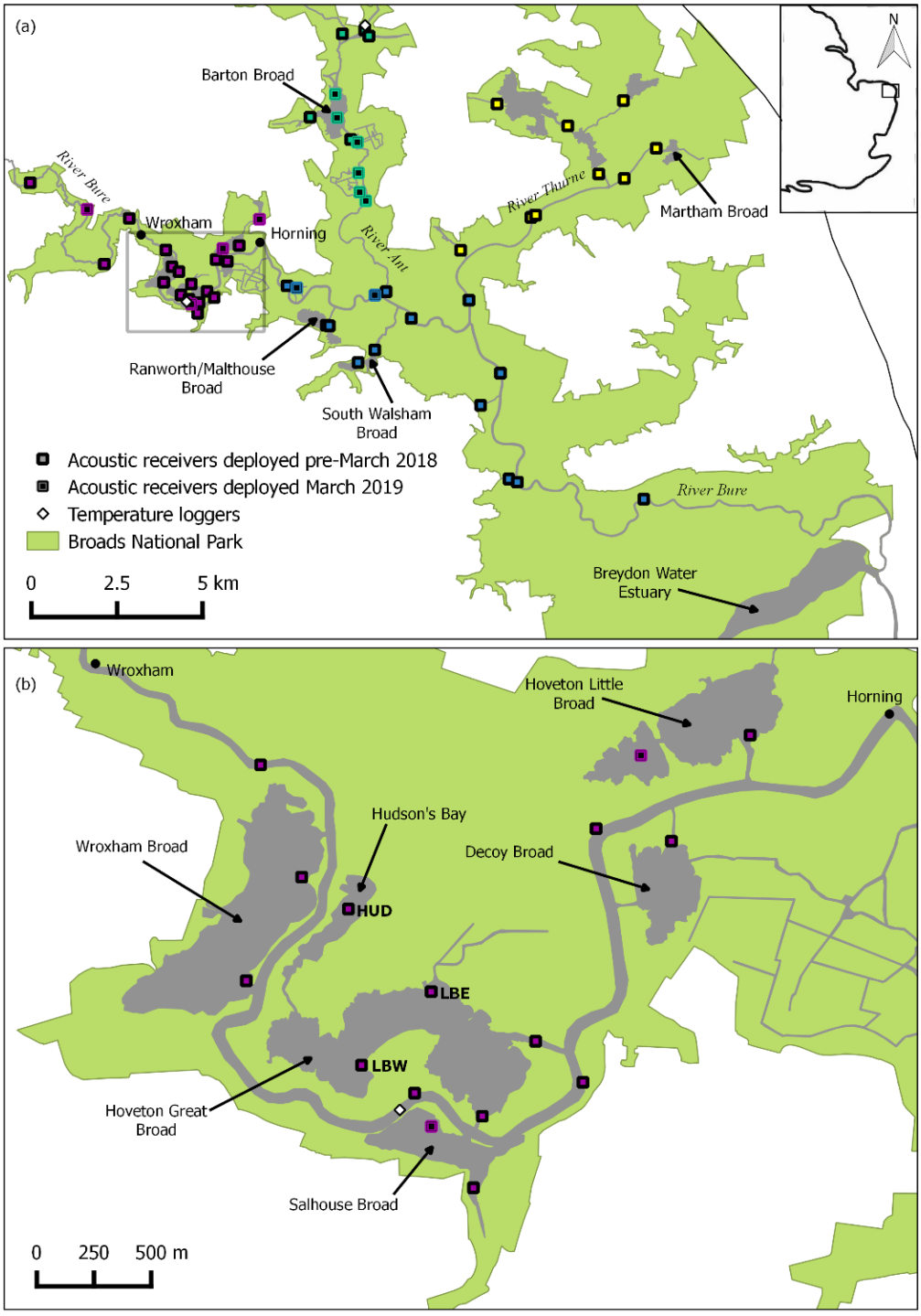

Figure 6.1: Map of the northern Norfolk Broads study system, comprising the Rivers Bure, Ant and Thurne and numerous connected lakes and dyke systems. The locations of acoustic receivers in the Upper Bure (purple), Lower Bure (blue), River Ant (green) and River Thurne (yellow) reaches are displayed, as are the locations of two temperature loggers. The rectangle in (a) indicates the spatial extent of the Wroxham-Horning river section illustrated in (b). Channel widths not to scale.

Table 6.1: Details of common bream sampling locations and tagging dates, along with sample sizes of those included in spatial and social preference analyses (residents & migrants only) for each yearly spawning period. Length is represented by the range of values, with mean ± SD in parentheses.

Sampling location	Tagging date(s)	N tagged	Length (mm)	2018 Analysis			2019 Analysis			2020 Analysis		
				N resident	N migrant	N other	N resident	N migrant	N other	N resident	N migrant	N other
Upper Bure	6 Nov 2017 – 8 Nov 2017	26	374 – 491 (435 ± 28)	13	-	-	3	-	-	2	-	-
Lower Bure	8 Nov 2017 – 9 Nov 2017	8	286 – 471 (362 ± 70)	-	-	3	-	-	-	-	-	-
Thurne	14 Jan 2018	17	341 – 471 (394 ± 32)	-	6	1	-	-	-	-	-	-
Ant	27 Jan 2018 – 29 Jan 2018	25	362 – 502 (406 ± 34)	-	3	12	-	1	4	-	-	2
Upper Bure	20 Apr 2018 – 23 Apr 2018	62	313 – 527 (413 ± 44)	-	-	-	25	15	3	16	11	-
Lower Bure	15 Sep 2018 – 18 Sep 2018	43	290 – 503 (389 ± 54)	-	-	-	2	6	6	2	2	1

6.3.4 Data preparation

The telemetry dataset was divided into reproductive periods and non-reproductive periods. In each year, the reproductive period was considered to commence on the first day when water temperature in the River Bure reached 9 °C, the rationale being that off-channel areas tended to be approximately 1 °C warmer than the main river channel, and this threshold likely captures bream movements just prior to the initiation of spawning at ≥ 12 ˚C (Backiel and Zawisza 1968). The reproductive period was considered to have terminated once the final migrant fish (see below) left the Upper Bure reach in a downstream direction. The daily number of fish detected at Hudson's Bay, a recognised long-term bream spawning location within Hoveton Great Broad (Figure 6.1b), provided an indication of spawning activity. Telemetry data from non-spawning periods were used to classify bream movement type but were otherwise excluded from further analyses. In addition, any bream that entered or were lost to the study during the spawning period were removed from the dataset for that year. This included fish whose acoustic detections ceased or became stationary, and for the 2018 dataset, included all bream tagged in April 2018 (Table 6.1).

6.3.5 Classification of movement type

Movement type was defined as follows: bream that overwintered (between 1 December and 28/29 February) exclusively in the Upper Bure reach and were then detected in the Upper Bure during the defined spring spawning period were classified as 'resident'; bream that overwintered either exclusively or partially outside the Upper Bure reach, but were then detected in the Upper Bure during the spring spawning period were classified as 'migrant'. A t-test and chi-squared test assessed whether fish length or sex differed by movement type (residency/ migration). Bream that did not enter the Upper Bure reach during the spawning period were classified 'other'.

6.3.6 Spatial preferences

The number of detections at each receiver gave an initial indication of 'hotspots' of bream activity. Detection count (minus false detections and detections from stationary tags) was scaled relative to the spatial area monitored by each receiver when detection range equalled 200 m. This was visualised for the year 2019 when sample sizes were greatest (Table 6.1) and when passive acoustic telemetry was supplemented by manual tracking and spawning surveys (Environment Agency, unpublished data). A measure of acoustic noise, the mean daily noise quotient, (Simpfendorfer et al. 2008) was calculated from summary data stored by the receivers and visualised alongside detection count. Negative values of the noise quotient indicated tag collisions, while positive values indicated ambient/ anthropogenic/ biotic noise.

Resident and migrant fish were then linked to the off-channel sites they visited in the Wroxham-Horning area in 'bipartite' networks. In these bipartite networks, fish and sites represented two types of nodes, with edges connecting fish to sites at which they were detected on a presence/absence basis. Separate networks were generated for each year. The sites examined were Wroxham Broad (WB; 2 receivers), Salhouse Broad (SB; 2 receivers), Hoveton Great Broad and Hudson's Bay (HGB; 3 receivers not including those on broad entrances), Decoy Broad (DB; 1 receiver) and Hoveton Little Broad (HLB; 2 receivers) (Figure 6.1b). However, SB was removed from the 2018 analysis due to concerns about the receiver detection range overlapping with the River Bure, with this receiver subsequently moved by approximately 100 m in August 2018 and therefore included in the 2019 and 2020 analyses. Site nodes were ranked according to common network metrics; 'degree' indicated the number of edges connected to a node (number of fish visiting), and 'betweenness' gave a measure of centrality based on the number of shortest paths travelling through a node (Farine and Whitehead 2015). For fish nodes, a generalised linear mixed model (GLMM) tested whether movement type (resident/migrant) and year predicted node degree (number of sites visited). This required a Poisson family structure, with fish ID included as a random effect. Between-individual variance was consistently

estimated as zero, so random effects were dropped from the model and data tested using a generalised linear model (GLM).

6.3.7 Social preferences

Bream co-occurrence was examined at the receiver(s) located at the highest-ranking site in the bipartite networks. The co-occurrence of individuals was defined as their simultaneous detection at the same receiver within the same hourly timestep. Detections at each receiver were examined separately, as were the years of study. Hourly timesteps greatly exceeded an acoustic tag's transmission delay, minimising the risk of false negatives, where fish were potentially not detected due to tag collisions or being slightly out of receiver detection range. Sampled timesteps were separated by intervals of 1-2 hrs to allow for re-organisation of the network and avoid temporal autocorrelation. Interval length alternated between 1 and 2 hrs so that timesteps were not continually sampled at the same time each day. Fish detected in 5 or more of the sampled timesteps were retained for co-occurrence analysis.

The strengths of association between individuals throughout each spawning period were then calculated using the Simple Ratio Index (SRI), where the number of timesteps that two fish co-occurred at a receiver was divided by the total number of timesteps where at least one of the individuals was detected at the same receiver. SRI ranged between 0 and 1, where 0 indicated individuals never co-occurred and 1 indicated they always co-occurred. SRI association strengths were accumulated into an association matrix, or network. To test if the observed association network was more differentiated than expected at random (i.e. more preferred/ avoided associations), the coefficient of variation (CV) of edge weights (SRIs) was compared to the CV of 50,000 randomised networks. Randomisation was achieved by rearranging the observed pre-network data stream, where with each permutation two individuals were swapped between co-occurrences, and the SRI association network was recalculated (Farine 2017). A p value was calculated as the proportion of times the CV of the observed network was less than the CV of the randomised networks.

A multiple regression quadratic assignment procedure (MRQAP), a method of matrix logistic regression for network data (Dekker et al. 2007), was used to test the influence of individual similarity between bream (length, sex, movement type) on their association strength. The SRI association network represented the dependent variable, while similarity matrices represented independent variables. Similarity was assessed on a binary scale, where a value of 1 indicated paired individuals were of the same sex, length class or movement type, and a value of 0 indicated their attributes differed. Length classes were defined as follows: < 400 mm, ≥ 400 mm. Null models were built from the data stream permutations described previously and applied using the *mrqap.custom.null* function within the *asnipe* package (Farine 2019) in R 4.0.2 (R Core Team 2020). Statistical analyses and data formatting also utilised the packages *igraph* (Csardi and Nepusz 2006) and *actel* (Flávio 2020).

6.4 Results

The three bream spawning periods were 26 March to 16 May 2018, 20 March to 26 May 2019 and 26 March to 17 May 2020 (Figure 6.2). The number of bream detected at Hudson's Bay, within Hoveton Great Broad (Figure 6.1b), generally peaked when the mean daily river temperature was approximately 15 °C (Figure 6.2). In 2019, these peaks of telemetry activity corresponded with direct observations of bream spawning activity in Hudson's Bay on 24-25 April and 16-19 May (Environment Agency, unpublished data; Figure 6.2).

After applying data restrictions, the 2018 dataset comprised the movements of 13 resident and 9 migrant bream, while the 2019 dataset comprised 30 residents and 22 migrants, and the 2020 dataset comprised 20 residents and 13 migrants (Table 6.1). For fish detected in multiple years, including those classified 'other' (n = 40), 88% were consistent in their type of movement behaviour (resident/ migrant/ other) across years. This included 36 bream that were detected in two consecutive years and 4 that were detected in three consecutive years. Across all resident and migrant individuals, length did not differ by sex (*t*-test: $t_{67} = 0.37$, $p = 0.72$), and, excluding bream showing flexible movement behaviour between years, length did not differ by

movement type (t_{67} = 0.49, p = 0.63). In addition, sex did not predict migratory tendency (χ^2 = 1.16, p = 0.28).

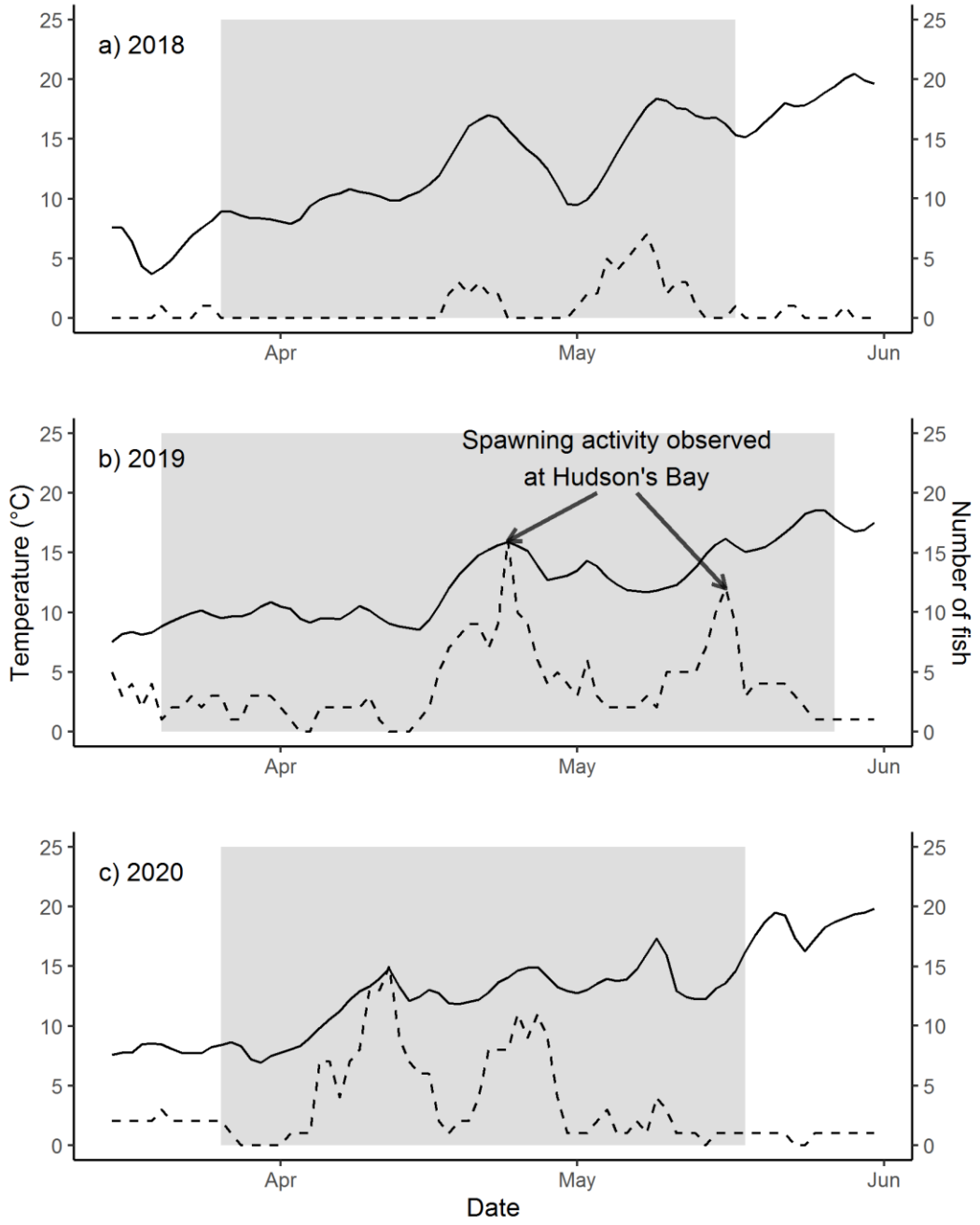

Figure 6.2: Mean daily temperature in the River Bure (solid lines) alongside daily number of fish detected at Hudson's Bay (dashed lines), a known bream spawning site within Hoveton Great Broad, in each year of study. River Bure temperature in (c) 2020 is estimated from River Ant temperature (see Methods). Spawning periods are shaded grey. Days in 2019 when spawning activity was directly observed at Hudson's Bay are illustrated in (b).

6.4.1 Spatial preferences

The total number of detections was highest for receivers situated in the Wroxham-Horning section of the Upper Bure, but was also relatively high at Ranworth/Malthouse Broad (Lower Bure), South Walsham Broad (Lower Bure), Barton Broad (River Ant) and close to Martham Broad (River Thurne) (Figures 6.1, 6.3). Detections at Ranworth/Malthouse Broad and Barton Broad were largely attributed to bream classified 'other' that did not visit the Upper Bure reach during the spawning period, while detections at Martham Broad were principally made by 'migrant' fish and those at South Walsham Broad were made by both 'migrant' and 'other' fish (Table 6.1; Appendix 5, Figures A5.1, A5.2, A5.3). Daily noise quotients ranged from -30,699 to 3,478, with 59 % of values lower than zero, indicating reduced receiver performance due to tag collision interference. This was particularly evident for receivers within Hoveton Great Broad (HGB), where detection count was likely considerably underestimated (Figure 6.3).

In the Wroxham-Horning river section, HGB consistently ranked highest of the site nodes in the bipartite networks according to degree and betweenness in all years (Table 6.2; Figure 6.4), indicating it was visited by the most fish and was the most central site within the networks. The GLM testing movement type on the number of sites visited in the Wroxham-Horning river section was significant, indicating that residents typically visited fewer off-channel sites than migrants (Table 6.3).

6.4.2 Social preferences

Co-occurrence analyses focused on the three acoustic receivers situated at HGB, excluding those located at the entrances to the broad (LBE, LBW & HUD; Figure 6.1b). A total of nine SRI association networks were examined across all years (Figure 6.5). In each network, fish nodes of opposite length class, sex and movement type were connected by edges, indicating the co-occurrence of bream with differing attributes at the same receivers within the same hourly timesteps (Figure 6.5). The null hypothesis that bream associated randomly was rejected for seven of the networks ($p \leq 0.001$), but at LBE and LBW in 2018 the observed coefficient of

variation (CV) was not significantly different to random (p = 0.20-0.30; Figure 6.5). This indicated that bream largely formed more preferred associations than expected at random. In some instances, MRQAP tests suggested that length, sex and/ or movement type were important predictors of association strength (Table 6.4), however given poor adjusted R^2 values and small effect sizes (< 0.05), the influence of these variables on the probability of co-occurrence at each of the receivers and in each year was considered relatively low.

Table 6.2: Off-channel sites in the Upper Bure ranked according to degree (number of fish detected) and betweenness (measure of centrality) calculated from bipartite networks. Rankings are provided in parentheses.

	2018		2019		2020	
	Degree	Betweenness	Degree	Betweenness	Degree	Betweenness
WB	12 (2)	90.9 (2)	11 (5)	146.5 (4)	8 (4)	56.4 (4)
SB	-	-	18 (3)	121.7 (5)	13 (3)	75.7 (3)
HGB	19 (1)	205.6 (1)	44 (1)	1105.9 (1)	26 (1)	405.5 (1)
DB	3 (4)	1.1 (4)	15 (4)	149.0 (3)	8 (4)	29.5 (5)
HLB	6 (3)	11.4 (3)	19 (2)	194.8 (2)	15 (2)	175.0 (2)

Note: WB = Wroxham Broad; SB = Salhouse Broad; HGB = Hoveton Great Broad; DB = Decoy Broad; HLB = Hoveton Little Broad

Table 6.3: Coefficient estimates (± SE) for the GLM predicting number of sites visited according to movement type and year. Estimates for migrants and the year 2018 are represented by the intercept.

Parameter	Fixed
(Intercept)	0.76 ± 0.17***
Type: Resident	-0.29 ± 0.14*
Year: 2019	0.12 ± 0.19
Year: 2020	0.16 ± 0.20

*** $p < 0.001$; * $p < 0.05$

Table 6.4: Results of the Multiple Regression Quadratic Assignment Procedures (MRQAPs) indicating the influence of bream similarity in length, sex and movement type on their association strength in each year and at each receiver (LBE; LBW; HUD) within the Hoveton Great Broad complex (Figure 6.1b). Regression coefficients (log odds) were considered significant (in bold) if greater than the null expectancy, thus when P ($|\beta| \leq |r|$) < 0.05. Receivers LBE and LBW were not included in the 2018 analysis as the SRI association networks were not considered significantly different to random.

Year	Receiver	N bream in network	Predictors	Regression Coefficient (β)	P ($\|\beta\| \leq \|r\|$)	Adjusted R^2
2018	HUD	6	Length	-0.014	0.65	-0.05
			Sex	**-0.040**	**0.041**	
			Type	-0.023	0.44	
2019	LBE	38	Length	-0.003	0.87	0.008
			Sex	0.005	0.08	
			Type	**0.021**	**<0.001**	
	LBW	29	Length	-0.009	0.35	-0.003
			Sex	**0.008**	**<0.001**	
			Type	0.003	0.11	
	HUD	16	Length	-0.007	0.12	-0.011
			Sex	0.011	1.00	
			Type	**-0.017**	**0.013**	
2020	LBE	24	Length	-0.009	0.13	0.017
			Sex	-0.0001	0.97	
			Type	**0.019**	**<0.001**	
	LBW	21	Length	-0.007	0.77	-0.007
			Sex	-0.004	0.90	
			Type	**0.011**	**0.025**	
	HUD	15	Length	-0.008	0.81	-0.026
			Sex	0.004	0.47	
			Status	0.0009	0.90	

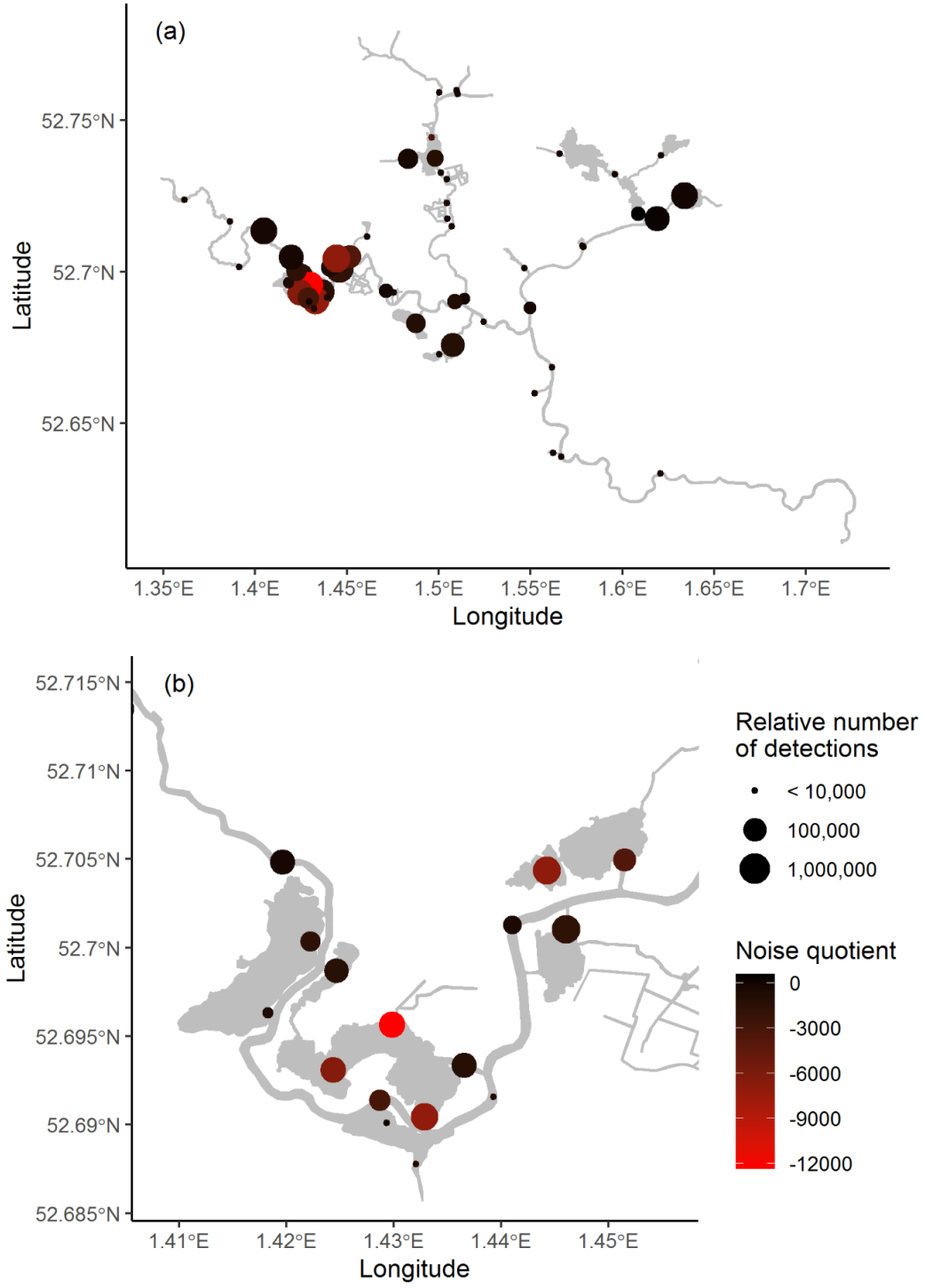

Figure 6.3: Total number of detections at each acoustic receiver during the 2019 spawning period (a) across the entire study area and (b) in the Wroxham-Horning section of the Upper Bure reach. Detections are scaled relative to the detection area of each receiver when detection range = 200 m. Points are coloured according to the mean daily noise quotient, with values < 0 indicating interference by tag collisions. Detections for fish classified 'resident', 'migrant' and 'other' are combined. See Appendix 5 for detection plots specific to movement type (Figures A5.1, A5.2, A5.3).

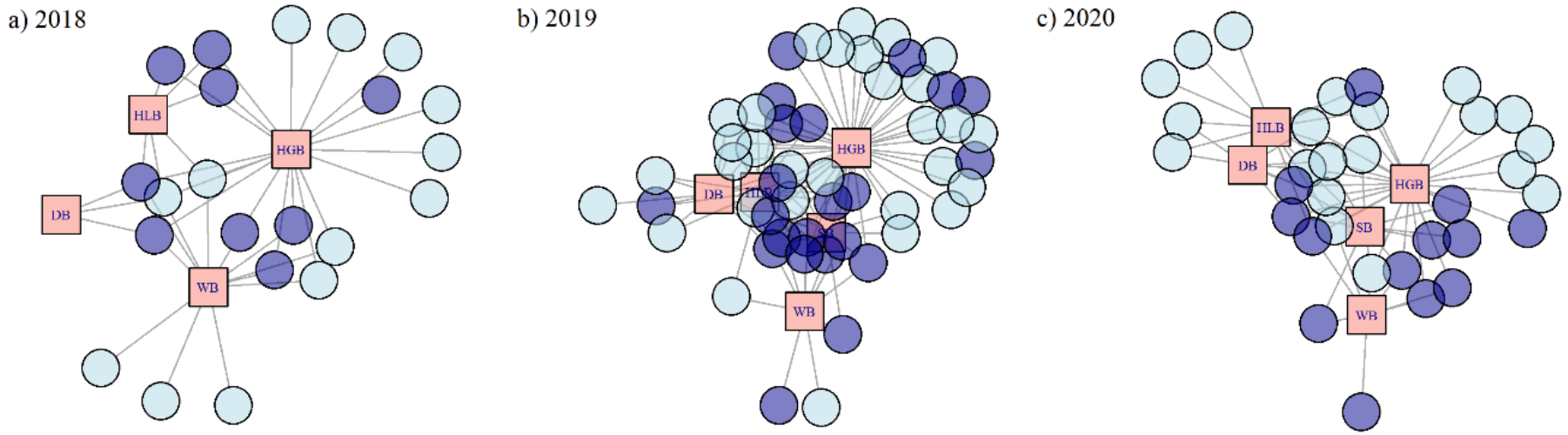

Figure 6.4: Bipartite networks of bream (circular nodes) linked to off-channel sites (square nodes) on a presence/ absence basis according to year of study. Circular node shading depicts bream movement type (light blue = resident; dark blue = migrant). WB = Wroxham Broad; SB = Salhouse Broad; HGB = Hoveton Great Broad; DB = Decoy Broad; HLB = Hoveton Little Broad.

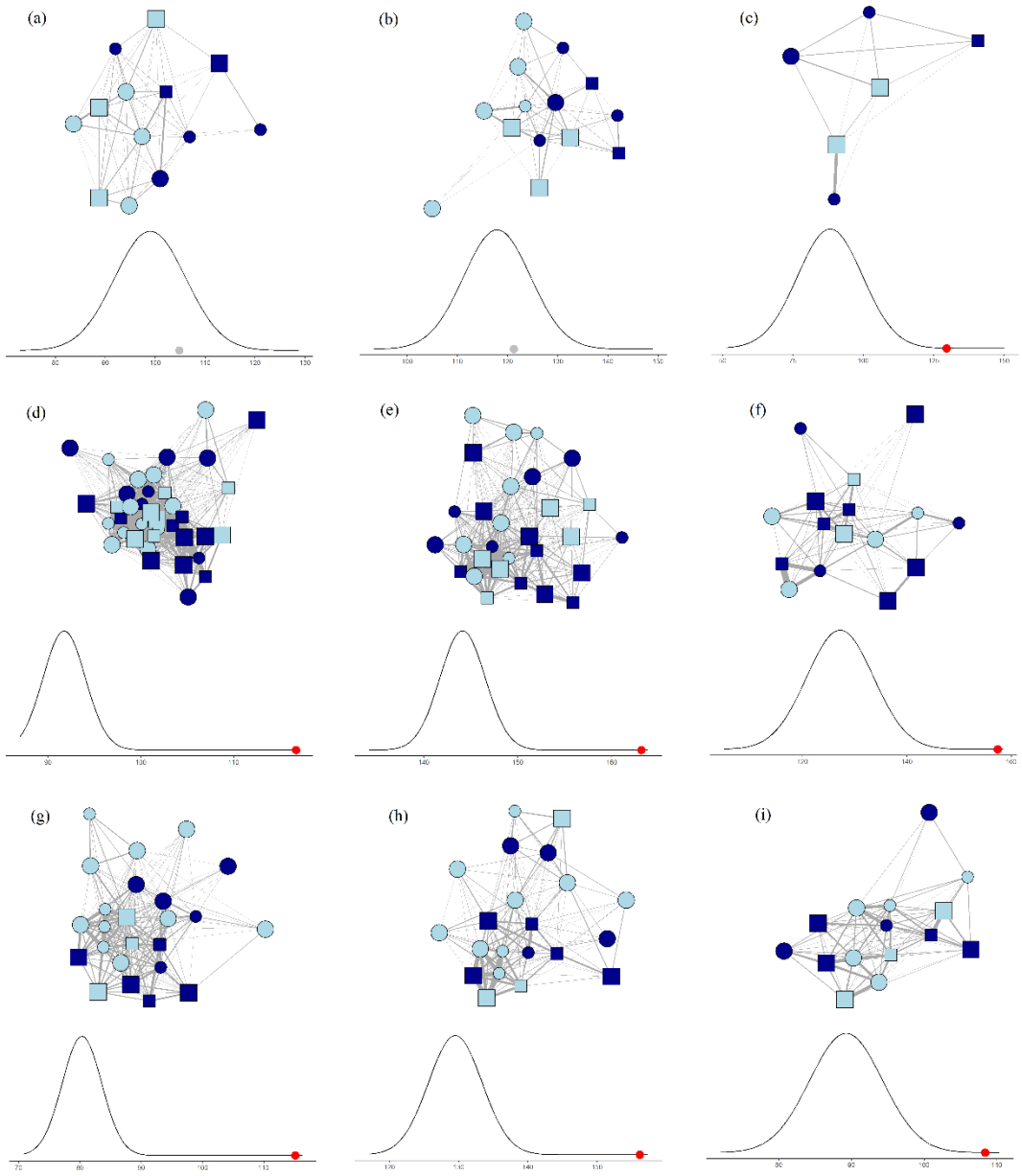

Figure 6.5: Common bream association networks at receivers located within Hoveton Great Broad: LBE (left; a, d, g), LBW (centre; b, e, h,) and HUD (right; c, f, i) in the years 2018 (top; a, b, c), 2019 (middle; d, e, f) and 2020 (bottom; g, h, i). Edge thickness is proportional to SRI values. Node shading depicts movement type (light blue = resident; dark blue = migrant), node shape depicts fish sex (square = male; circle = female) and node size depicts fish size (small: < 400 mm; large: ≥ 400 mm). Each panel displays the observed network (top) and the normal probability density plot for the coefficient of variation (CV) values of the 50,000 random networks (bottom). In the density plots, values of the observed CV are indicated by dots (red = statistically significant; grey = non-significant).

6.5 Discussion

Through applying passive acoustic telemetry in a well-connected wetland system, this study revealed a high consistency in the movement phenotypes of common bream and revealed that, despite resident and migrant sub-populations being spatially discrete in non-reproductive periods (Chapter 5), they did mix in space and time during their reproductive period. The potential for their interbreeding during spawning was thus considered to be high, suggesting that the different phenotypes comprised a single metapopulation that converged at particular off-channel sites to reproduce on an annual basis.

The tagged bream showed high consistency in their movement behaviour (residency/ migration) across the three annual reproductive periods. Brodersen et al. (2014) also documented high individual consistency in the movement phenotype of *R. rutilus*, with a high somatic condition increasing the likelihood of individuals adopting the migration strategy (see also Brodersen et al. 2008). Conversely, evidence suggests that habitat shifts of bream are more likely to occur in fish of low somatic condition (Brodersen et al. 2019), although how condition during juvenile development and maturation affected the subsequent behaviour of the adult fish here was unable to be tested. Indeed, behaviourally plastic traits in early life may become canalised and fixed in certain individuals, dependent on genetic and environmental threshold states (Chapman et al. 2012a, Brodersen et al. 2014). Consequently, adopting long-term studies on the movements of bream that encompass both their juvenile and adult life stages would be helpful in identifying the ecological mechanisms by which individuals adopt different behavioural strategies. There are, however, technological issues to overcome here relating to the type of tags used, and their lifespan and suitability for implanting into juvenile fish. Notwithstanding, studies increasingly suggest that some smaller tags can be used on relatively small fish without long-term detrimental impacts on their growth and survival (Crossin et al. 2017, Klinard et al. 2018).

It is highly likely that detection count was underestimated where acoustic interference due to tag collisions was high. Sporadic use of mobile tracking and side scan sonar imaging in the Wroxham-Horning reach during 2019 confirmed that,

where bream were densely aggregated, tag collisions contributed to missed and false acoustic transmissions (Environment Agency, unpublished data). There exists a trade-off between maximising the temporal resolution of acoustic tracking (by reducing transmission delay) and minimising the risk of tag collisions (by increasing transmission delay) (Simpfendorfer et al. 2015). Similarly, the risk of tag collisions increases with the sample size of tagged fish. For example, with a random transmission interval ~ 90 s and an acoustic pulse time of ~ 3 s (time required to transmit signal), an aggregation of 30 tagged individuals within range of one receiver could result in almost continuous interference. Thus, without the use of controls (e.g. fixed-location sentinel tags), metrics dependent on receiver performance should be interpreted with caution (Payne et al. 2010). However, a new digital coding system, with a transmission time of < 1 s, is less sensitive to acoustic noise and shows potential for more efficient monitoring of dense aggregations of tagged animals (Guzzo et al. 2018, Leander et al. 2020).

In most cases, the co-occurrence of bream at acoustic receivers was not random, suggesting the existence of distinct shoals, with certain individuals more likely to be detected simultaneously than expected by chance. This is in line with their known gregarious nature (Backiel and Zawisza 1968). However, the probability of co-occurrence was not strongly correlated with similarity in fish length, sex or movement type (resident/ migrant). Other species of shoaling fishes can show strong segregation by sex and/ or body size, including during spawning, for example Atlantic cod *G. morhua* (Morgan and Trippel 1996). Others may be grouped according to behavioural type, which may link to physiological differences, such as activity levels or environmental tolerances (Killen et al. 2017). One possibility not examined here is the segregation of fish by relatedness, which may be more relevant during reproductive periods than at other times of the year (Ward et al. 2020). Assortative mating could be contributing to phenotypic expression, however the acoustic telemetry technology used here was unsuitable for monitoring fine-scale spatial (< 1 m) and temporal (< 5 s) interactions between fish. Elsewhere, assortative mating is thought to influence the genetic and morphological divergence of roach and European perch *Perca fluviatilis* across the littoral-pelagic axis (Faulks et al. 2015), as well as the trophic morphology of three-spined stickleback *Gasterosteus aculeatus* (Garduno-Paz et al. 2020). Thus, newly available advanced positioning

telemetry could be applied to testing this in wild bream (Guzzo et al. 2018, Leander et al. 2020).

There was also no statistical difference in the lengths of migrant and resident bream at tagging. Evidence from other studies suggests that smaller individuals (across the length range of 100 to 550 mm) have a higher propensity to migrate between habitats (Skov et al. 2011). That such an effect was not detected in the present study could have been an artefact of the study design, as the use of the acoustic tags precluded the tagging of fish below 290 mm. Whilst the findings of Skov et al. (2011) imply that bream movement occurs across a gradient of predation risk, in the Norfolk Broads study area piscivorous fish (e.g. Northern pike *Esox lucius*), birds (e.g. cormorant *Phalacrocorax* spp.) and mammals (e.g. otter *Lutra lutra*) are present throughout the study system. This suggests that the partial migration of bream observed here was driven less by predation vulnerability and more likely by trophic polymorphism, where migrants that overwinter in the brackish reaches of the study area (i.e. the Lower Bure & River Thurne) will specialise on different prey to those in upstream areas (Chapman et al. 2012a). A recent study suggested that the diet composition of bream is sex-specific, although this did not coincide with sexual segregation in habitat use (Žák et al. 2020). In the present study, migratory phenotype was not related to sex.

During the reproductive period, sympatric resident and migrant phenotypes co-occurred in space and time, indicating the potential for their interbreeding and suggesting the phenotypes comprised one larger metapopulation. This lack of spawning segregation implies that bream life history is at least partly influenced by extrinsic factors, such as population density or resource availability, although gene flow between the phenotypes could still be limited through post-zygotic selection against resident-migrant hybrids (Turbek et al. 2018). This could manifest in a higher mortality of the intermediate behavioural type, as observed in hybrids of bird species navigating around unsuitable geographic areas (e.g. Delmore and Irwin 2014) and in roach/bream hybrids that are more vulnerable to predation (Pärssinen et al. 2020). Ultimately, the phenotypic diversity observed here likely promotes long-term population stability through buffering against site-specific mortality due to environmental fluctuations (Chapman et al. 2012a). These inferences suggest that

assessment of the role of these spawning and non-spawning behaviours and movements would be strongly informed by complementary population genetic analyses.

The presence of different migratory strategies within populations of cyprinid fishes is becoming increasingly evident, with the phenotypic diversity demonstrated in this bream population being similar to that detected in populations of other cyprinid species, such as *R. rutilus* (Chapman et al. 2012b, Brodersen et al. 2014). Thus, where high habitat connectivity has been maintained in freshwater systems, then life history strategies that encompass partial migration are usually preserved. Yet evidence suggests that globally, there are few rivers that remain free flowing throughout their length (Grill et al. 2019) and in Great Britain, only 3.3 % of the total river network remains fully connected (Jones et al. 2019). Consequently, if it is considered that maintaining this phenotypic diversity in cyprinid species is an ecological and conservation priority, given its potential importance for maintaining genetic diversity and population stability, then this can only be achieved by prioritising the maintenance and/ or restoration of functional habitat connectivity in lowland river systems.

7 General discussion

7.1 Overview of thesis

Rivers with heterogeneous habitats and considerable lateral and longitudinal connectivity support a high diversity of fauna and flora (Pander et al. 2018). However, the maintenance of habitat complexity and connectivity has become increasingly rare in contemporary freshwater landscapes (e.g. Jones et al. 2019), and relatively few research projects have addressed non-salmonid fish movement ecology in such systems. Exploring the natural variation in behaviours of fishes is inherently challenging, but is important for informing aquatic conservation and restoration (Kessel et al. 2018, Kärgenberg et al. 2020). For ichthyologists, continued advances in acoustic biotelemetry offer a 'window into the underwater world' (Hussey et al. 2015) and have now been widely applied to fish in freshwater systems (Cooke et al. 2013, Crossin et al. 2017). The aim of this research was to investigate the spatial and temporal variability in the movements of a lowland river fish and explore its ecological implications. Common bream provided a strong model species for analysing intraspecific diversity in potamodromy, given their capacity for migration over distances exceeding 60 km (Backiel and Zawisza 1968, Whelan 1983, Lucas and Baras 2001). In addition, the Broads National Park ('Broads') of eastern England provided an appropriate lowland wetland system in which to examine unconstrained fish movement, given its large network of interconnected rivers, lakes and dykes (Broads Authority 2018).

Initially, the focus was on assessing the applicability of acoustic telemetry to studying the movement behaviour of lowland fishes, through quantifying acoustic receiver performance (Chapter 2) and the survival of fishes post-tagging (Chapter 3). Then, understanding the value of an alternative 'isoscape' tracking technique to complement acoustic telemetry in lowland systems involved performing and interpreting stable isotope chemistry from across a wide spatial area (Chapter 4). Finally, to investigate the movement ecology of bream over successive years, including the extent of population mixing throughout the Broads system, acoustic telemetry data were analysed with respect to year-round seasonal behaviour (Chapter

5), and reproductive behaviour more specifically (Chapter 6). This chapter synthesises the results of the thesis in order to make recommendations for best practice field methods and data interpretation, to draw general conclusions regarding the diversity, repeatability and ecological implications of bream migration behaviour specifically and fish behaviour more generally, and to highlight remaining questions that could not be resolved by this work.

7.2 Aquatic acoustic biotelemetry: limitations and implications

In Chapter 2, the detection range and efficiency of fixed-location acoustic receivers was assessed using the detections of stationary tags (lost from fish due to mortality or expulsion) and complementary boat-based testing. While both detection metrics were temporally variable, they were strongly predicted by water temperature, transparency and/ or precipitation. These findings complement the growing body of literature quantifying acoustic receiver performance across environmental gradients (Kessel et al. 2014b, Huveneers et al. 2016, Brownscombe et al. 2020), including studies that attribute increased sound attenuation (and thus poor receiver performance) to high turbidity or the entrainment of air bubbles by wind and rain (Shroyer and Logsdon 2009, Gjelland and Hedger 2013). Nevertheless, few studies have addressed long-term temporal variation in detection range (over 12+ months; but see Hayden et al. 2016), yet the results here highlight the dependence of receiver performance on seasonally fluctuating conditions. This is important, as range tests conducted infrequently or in limited periods (e.g. days or weeks prior to study onset) may not always reflect true system performance. In lowland eutrophic rivers, where seasonally abundant phytoplankton can form dense blooms (Figure 7.1; Moss and Balls 1989), this may result in insufficient monitoring of tagged fish at receiver gates or curtains at certain times of the year.

Figure 7.1: An example of a dense algal bloom in the River Bure system that resulted in high turbidity. Photograph taken on 03/08/2018.

The use of seasonally variable tag transmission intervals (i.e. shorter intervals when detection range predicted to be low) could help to resolve issues around inconsistency of receiver performance. However, the efficacy of this measure would diminish in situations where receiver performance is less predictable, such as during periods of increased turbidity that follow stochastic episodes of heavy rainfall (Chen et al. 2018). A more comprehensive monitoring approach would be to deploy 'control' sentinel tags (Kessel et al. 2014b, Selby et al. 2016, Brownscombe et al. 2020), but where this is unfeasible, due to cost or study system characteristics, continuous measures of key predictor variables should be complemented by frequent, regular range tests.

Acoustic noise is known to impact receiver performance and data interpretation (e.g. Payne et al. 2010), and noise quotients calculated from summary receiver metadata (Chapters 2 and 6) suggested a high incidence of interference due to collisions of tag transmissions from tagged fish (Simpfendorfer et al. 2008). Despite this, noise was not a strong predictor of the detection efficiency of stationary tags (Chapter 2), but was considered highly likely to have contributed to reduced detection frequency of bream at key sites of aggregation during the spawning period (Chapter 6). For future studies testing detection efficiency, a better measure of noise may be the number of

detections by transmitters other than the reference tag (Brownscombe et al. 2020), although this would theoretically reach a maximum and then begin to decline over and above a threshold of tag abundance. For studies tracking large numbers of highly gregarious animals, adopting the new 'high-residence' type of acoustic telemetry coding scheme, with ID codes transmitted in <10 ms, could overcome the risk of signal collision and improve detection efficiency (Guzzo et al. 2018, Leander et al. 2020). Nevertheless, this approach generates extremely large datasets that can require complex algorithms for interpretation (Vergeynst et al. 2020).

With the post-acoustic tagging survival of fishes examined in Chapter 3, it was concluded that bream were lost at a higher rate than expected by natural mortality alone. This contributed to reduced sample sizes for subsequent evaluations, with less than 50 % of the tagged bream detected for sufficient time for inclusion in the analyses of Chapter 4. Furthermore, only 20 % of tagged bream were detected across two consecutive spawning periods (Chapters 5 and 6) and 5 % of those tagged prior to April 2018 were detected across three consecutive spawning periods (Chapter 6). Previous acoustic telemetry studies on bream have not reported such significant rates of loss (Lyons and Lucas 2002, Le Pichon et al. 2017), although Gardner et al. (2013) noted an average tracking duration of less than one year for bream, and were the only other researchers to make use of larger tags (Vemco, V13; also used here). Nevertheless, these transmitters are still within the accepted tag mass: body mass ratio and multiple studies have exceeded the generally accepted 2% limit without compromising fish condition or survival (Jepsen et al. 2003; Newton et al. 2016), including for a laterally compressed fish species (Klinard et al. 2018).

The fate of fish following tagging is important to consider, as adverse effects on behaviour and survival should be minimised (e.g. Bolland et al. 2019), and the measured behaviours should be representative of the wider untagged population (Bridger and Booth 2003). Yet, this is often overlooked in acoustic telemetry research (Klinard and Matley 2020). Transmitters with integrated sensors can aid in determining the fate of tagged animals (Villegas-Ríos et al. 2020), including through identifying predation events (Halfyard et al. 2017, Klinard et al. 2019b), with the selective predation of tagged fish by mammals that can sense acoustic tag signals

potentially being a problem ('dinner bell' effect; Rub and Sandford 2020). Notably, the Eurasian otter *Lutra lutra*, a predator of bream in the Broads, has similar auditory thresholds to the California sea lion *Zalophus californianus* (Voigt et al. 2019), a predator species featured in Rub and Sandford's (2020) report. But despite technological advances that can enable greater certainty of the fate of tagged animals, studies that result in high loss rates are not cost-effective and raise issues around fish welfare and research ethics (Wilson and McMahon 2006, Heylen and Nachtsheim 2018).

The results of Chapter 3 can inform and improve future tagging protocols for bream specifically, and fish more generally. The results clearly demonstrated that avoiding the surgical implantation of tags during autumn and winter periods resulted in reduced loss rates. This is contrary to the traditional practice of tagging fish in cooler temperatures or in the lower range of their physiological tolerances (Jepsen et al. 2002, Cooke et al. 2011). This custom is based on evidence that warmer temperatures can enhance infection rate, amplify the stress response and increase mortality, particularly in salmonid fish (Strange et al. 1977, Walsh et al. 2000, Deters et al. 2010, Yasuda et al. 2015). Nevertheless, with fish tagged in cooler climates, suture material (mostly designed for use in endotherms) can take more than two years to dissolve, impacting inflammation and irritation at the incision site, and thus potentially resulting in higher rates of secondary infections (Schoonyan et al. 2017).

In the Broads study system, survival was significantly greater for bream tagged in spring, when water temperatures were above 15 °C, and just prior to their spawning. However, water temperatures during tagging may not have been the limiting factor here, as bream tagged in the month of September, also at temperatures above 15 °C, had a similar rate of loss to those tagged during cooler months. Thus, survival, and perhaps the retention of acoustic tags, may be dependent on seasonal physiological changes within the fish. The risk of tag expulsion in bream is potentially also linked to the size of acoustic tags (Welch et al. 2007), but this could not be tested here due to too few bream (<5 %) being tagged with smaller transmitters (Vemco, V9). The recapture of acoustic-tagged bream by Gardner et al. (2015b) highlighted their capacity for advanced healing and external recovery, although there was the

possibility that recaptured individuals that had lost tags may have been missed and, therefore, a dedicated tag retention experiment, with different sized tags, would be beneficial to inform future studies on the species. Concurrently, for the tracking of bream in the wild, the coupling of acoustic telemetry with passive integrated transponder (PIT) telemetry should be considered as important in order to ensure mortality is not overestimated (Chapter 3).

7.3 Utility of multi-isotope isoscapes for freshwater systems

The geographic assignment of roach *Rutilus rutilus* and bream stable isotope (SI) signatures to their most likely origin was conducted using continuous-surface models of isotopic landscapes ('isoscapes'; Chapter 4). This likelihood-based approach takes SI measurements at known locations and estimates SI ratios throughout the landscape by interpolation, which, in combination with measures of biological variance and model uncertainty, can be used to calculate spatially explicit probabilities of animal origin (e.g. Vander Zanden et al. 2015a). The development of multi-isotope isoscapes (as opposed to single-isotope isoscapes) is relatively novel and has not previously been applied to freshwater systems, yet applications to terrestrial and marine environments have shown enhanced predictive power (Hobson et al. 2012, Vander Zanden et al. 2015a, Torniainen et al. 2017). The results of Chapter 4 revealed that assignment error for roach was reduced when using the dual-isotope method ($\delta^{13}C$ and $\delta^{15}N$) compared to the single-isotope ($\delta^{13}C$ only) method. However, the resolution remained low compared to the accuracy and precision of acoustic telemetry, as has been identified in other studies (Vander Zanden et al. 2018, Coffee et al. 2020). Indeed, the isotope tracking of organisms at increasingly fine spatial scales remains a significant challenge, especially where baseline isotopic values show low variability over large spatial areas (McMahon and Newsome 2019).

Nevertheless, for lowland river and estuarine species that cannot be tracked electronically, riverine isoscapes do offer potential for uncovering foraging movements in freshwater. For example, quantifying the extent of catadromy in juvenile anguillids is often reliant on analysing otolith microchemistry that requires lethal sampling (e.g. Harrod et al. 2005, Daverat et al. 2006), which is increasingly

difficult to justify with global eel populations being imperilled (Jacoby et al. 2015). Yet, the application of stable isotope analysis of fin tissue can reveal seasonal habitat shifts of eels that otherwise go undetected by otolith microchemistry (Clément et al. 2014). Thus, the combined used of non-invasive tissue sampling with dual-isotope isoscapes could improve the spatial and temporal resolution of their tracking, whilst also avoiding the euthanasia of species of high conservation concern (Jacoby et al. 2015), and potentially reducing the sample size requirements of fish to be fitted with electronic tags (Thorstad et al. 2013). Extending the method to full catchment-scale tracking is also possible, provided SI ratios are spatially heterogeneous between river reaches, although in the absence of tidal flux, the hierarchical, dendritic nature of freshwater hydrology may need to be considered (Brennan and Schindler 2017).

Recent advances in refining isoscapes for animal tracking have involved the use of compound-specific SI analysis, as opposed to analysis of bulk tissues composed of various types of molecules (McMahon and Newsome 2019). The principal benefit is that $\delta^{13}C$ and $\delta^{15}N$ at the base of the food web can be calculated from amino acid SI ratios, regardless of animal trophic position or tissue-specific fractionation, meaning the accuracy and precision of isoscape tracking can be improved (Larsen et al. 2020, Matsubayashi et al. 2020). Furthermore, the combined use of carbon, nitrogen, hydrogen, oxygen or strontium SI ratios (Hobson et al. 2012, Brennan and Schindler 2017, Torniainen et al. 2017) with more novel tracers, such as neodymium (Saitoh et al. 2018) and radiocarbon (Larsen et al. 2018), offers further diversity for multi-isoscape models, potentially enhancing their applicability across a wide range of freshwater systems. The main drawback in expanding the range of analytical techniques for any single project is expense, and when coupled with a requirement for expertise in data interpretation, particularly for compound-specific SI analysis, novel methods may currently serve more value in supplementing traditional isoscape tracking than in redefining analytical approaches (McMahon and Newsome 2019).

7.4 Movement ecology of bream in a highly connected wetland

Studies increasingly suggest that highly connected freshwater systems support fish communities with greater inter- and intraspecific biodiversity, including in their behavioural phenotypes (Liu and Wang 2010, Kessel et al. 2018, Thompson et al. 2019, Kärgenberg et al. 2020). When unconstrained, the movement of fish can vary in terms of timing (Winter et al. 2016), distance travelled (Hess et al. 2014), and/ or the habitat destination (Kessel et al. 2018). Furthermore, the level of consistency or plasticity in movement tendency may be specific to individuals (Brodersen et al. 2014). In dispersing individuals heterogeneously across space and time, these forms of partial migration influence the ecology, productivity and viability of populations (Chapman et al. 2012a).

In the northern area of the Broads National Park, the tagged bream population was widely dispersed for most of the year, but with the ranges of individual fish being more spatially restricted. In entirety, this indicated the population was comprised of several spatially distinct sub-populations (Chapter 5). Among individuals, movement tendencies were highly variable, with some fish remaining in confined areas year-round, while others performed repeated migrations of up to ~25 km between overwintering and spawning habitats (Chapters 5 and 6). Given their capacity for migration over 60 km (Lucas and Baras 2001), this suggests an abundant availability of suitable functional habitats for bream within this lowland wetland, as opposed to less naturalised systems that have been heavily modified by anthropogenic activities (Gardner et al. 2015a). Behavioural variation likely then strengthens the population by allowing individuals to exploit spatially variable resources and buffering against localised stressors (Chapman et al. 2012a). The converging of bream sub-populations during the spring spawning period indicated the potential for interbreeding between these sub-populations, implying residents and migrants comprised one single metapopulation, although this was not tested directly (Chapters 5 & 6). Thus, extrinsic factors are perhaps more than or equally as influential as genetic differentiation in the adoption of a migratory strategy in bream, such as is the case for white perch *Morone americana* (Kerr and Secor 2012), roach (Brodersen et al. 2014) and brown trout *Salmo trutta* (Rodger et al. 2020). This has implications for

population stability, with genetically connected populations having greater resilience to disturbances such as disease or extreme environmental conditions (Jousimo et al. 2014, Christie and Knowles 2015). For example, should the component of the Bure bream population that resides in the lower, brackish reaches be impacted by saline intrusion (BBC 2014), or a toxic bloom of *Prymnesium parvum* (ITV 2015), the subsequent production of migrants from the upper reaches would be predicted to recolonise these affected areas (Pickett and White 1985).

Given that the spawning of residents and migrants was not explicitly observed, the results of this project could be complemented with an analysis of genetic population structure, to assess the extent of gene flow between bream behavioural phenotypes. This would clearly demonstrate the extent of their mixing during spawning and whether these fish act as a metapopulation within the northern Broads study area. Previously, genetic differentiation has been identified for populations of bream from within the same river system (Fuchs et al. 1998), although the outcome of genetic analysis for this species can depend heavily on the choice of genetic marker (Hayden et al. 2011). In some systems, bream also spawn in multiple 'batches', in different locations during one reproductive season (Targońska et al. 2014; German, 2019). While the extent of batch spawning is unknown in the Broads system, it could impact the degree of reproductive isolation between residents and migrants, by increasing the potential for promiscuity. This might be expected to reduce the genetic differentiation of behavioural phenotypes (D'Urban Jackson et al. 2017). Indeed, in brown trout, another species displaying facultative migration, genetic divergence tends to be associated with geographic location, rather than life-history strategy (Rodger et al. 2020).

Other non-salmonid, potamodromous fishes show high behavioural diversity in their habitat use and migration tendency in connected systems, including lake sturgeon *Acipenser fulvescens* (Kessel et al. 2018) and asp *Leuciscus aspius* (Kärgenberg et al. 2020). The advent of aquatic biotelemetry has revealed partial migration in many species whose behavioural phenotypes are morphologically indistinct and that were formerly considered sedentary (Brodersen et al. 2008, Kerr et al. 2009). Consequently, it is increasingly recognised that the maintenance of such intraspecific

diversity is an important conservation goal, including where different phenotypes are derived from the same gene pool (Blanchet et al. 2020), but this has generally been overlooked in population and evolutionary models (Bowler and Benton 2005). Moreover, managing the habitat requirements of partially migrant populations is considerably more complex than for spatially distinct and well-defined populations. Thus, it is highly likely that many migratory or highly vagile phenotypes have suffered unknown declines in response to habitat degradation and fragmentation, but gaining a deeper understanding of behavioural diversity through the tracking of multiple individuals could inform and improve future fisheries management (Chapman et al. 2012a).

Through the combination of dual-isoscape tracking and acoustic telemetry, bream home ranges appeared repeatable among years (Chapter 4). This was supported by high consistency in spatial occupancy and migratory tendency across the multiple years of acoustic telemetry (Chapters 5 and 6), suggesting that residency and migration form alternative life-history strategies for bream (Backiel and Zawisza 1968, Whelan 1983). However, the inability of the isoscapes to predict the subsequent directionality of movement recorded by telemetry could also represent a degree of nomadism or plasticity in summer foraging preferences of bream (Chapter 4; Brodersen et al. 2019), despite the summer season being generally characterised by reduced home ranges (Chapter 5). This intraspecific behavioural diversity is likely a consequence of the system's characteristically high habitat connectivity. Consequently, the introduction of barriers to bream movements in the Bure system, whether physical or physiological (e.g. saline limit), could result in reduced variation in life-history strategies and individual behaviours (e.g. Thompson et al. 2019).

The social preferences of bream were explored in Chapter 6, but technological limitations meant fine-scale interactions between individuals could not be distinguished. Elsewhere, animal interactions have been explored using animal-borne tag-receiver units, such as the Vemco Mobile Transceiver that records the presence of other nearby transmitters (VMT; Lidgard et al. 2012, Barkley et al. 2020), as well as using a newly available advanced positioning type of acoustic telemetry (Guzzo et al. 2018, Leander et al. 2020). This technology, coupled with the long-term tracking

of juveniles, could be useful in investigating the causes of partial migration within this bream population (e.g. Skov et al. 2011, Chapman et al. 2012a, Brodersen et al. 2014). Indeed, what remains to be explored is whether the selection of specific overwintering, spawning and summer foraging habitats is learned from older, experienced individuals, or represents an innate type of random dispersal (MacCall et al. 2019). With the former, habitat preferences of fish may be more unpredictable following disturbance, due to the loss of elders and cultural knowledge from the population, such as with bluehead wrasse *Thalassoma bifasciatum* (Warner 1988) and Atlantic herring *Clupea harengus* (Oskarsson et al. 2009), that showed variation in their habitat selection following experimental manipulation or stock collapse. This is important, as bream are ecological engineers, and their presence can be linked to increased turbidity and eutrophication in shallow lakes (Breukelaar et al. 1994, Hansen et al. 2019a). Thus, population disturbance in one area could drive the evolution of a new behavioural strategy, with unpredictable consequences for aquatic ecology in neighbouring reaches (Brodersen et al. 2019).

Within the Broads study system, the Upper Bure reach, and more specifically Hoveton Great Broad (HGB), has been identified as important for bream overwintering and spawning (Chapter 6; Environment Agency, unpublished data; Hindes 2019). Nevertheless, HGB is likely to soon be disconnected from the wetland system, with the additional planned removal of cyprinid fish as part of a biomanipulation programme aimed at restoring its water quality and biodiversity (Moss et al. 1996, Environment Agency 2020a). Monitoring the response of the bream population to this sudden loss of lateral connectivity presents an interesting opportunity for future applied and theoretical research, including regarding its effects on the expression of resident and migratory phenotypes. In removing access to a key functional habitat, the isolation of HGB will likely enhance bream population abundances in neighbouring off-channel habitats that, if resources become limited, could drive an increased production of migrants (Chapman et al. 2012a). For example, food availability and body condition has been shown to influence migratory tendency in roach (Brodersen et al. 2008, Brodersen et al. 2014) and brown trout (Wysujack et al. 2009). Alternatively - or concurrently - resident fish in the Upper Bure may exhibit a competitive advantage over migrants in the selection

of suitable remaining spawning habitat, such that migrant fish are displaced elsewhere to reproduce, potentially impacting gene flow between the behavioural phenotypes (Turbek et al. 2018). Ultimately, monitoring the responses of bream to this disturbance could be highly informative for deciphering the ecological and evolutionary mechanisms driving partial migration.

7.5 Conclusions

In summary, this thesis has provided insight into the efficacy and methodological limitations of acoustic telemetry and isoscape tracking when applied to freshwater fish in a lowland wetland system. Further, regarding a species of high importance to the recreational angling community, but which has rarely been comprehensively studied in a well-connected, naturalised environmental context, these results revealed quantitative evidence of diverse behavioural strategies (partial migration) in a system with few barriers to fish movement. This highlights the importance of habitat connectivity to maintaining intraspecific diversity, which should influence more informed management and conservation practices in fragmented or degraded systems. Future avenues of research, detailed above, could be used to improve best practice monitoring of common bream and other species, and expand current knowledge and understanding of the ecological causes and implications of behavioural diversity in fishes.

References

Adams, B. K., Cote, D. and Hutchings, J. A., 2016. A genetic comparison of sympatric anadromous and resident Atlantic salmon. *Ecology of Freshwater Fish*, 25 (2), 307-317.

Alós, J., Palmer, M. and Arlinghaus, R., 2012. Consistent selection towards low activity phenotypes when catchability depends on encounters among human predators and fish. *Plos One*, 7 (10), e48030.

American Rivers, 2019. *American Rivers Dam Removal Database*. figshare.

Ammann, A. J., 2020. Factors affecting detection probability and range of transmitters and receivers designed for the Juvenile Salmon Acoustic Telemetry System. *Environmental Biology of Fishes*, 103 (625-634).

Ammann, A. J., Michel, C. J. and MacFarlane, R. B., 2013. The effects of surgically implanted acoustic transmitters on laboratory growth, survival and tag retention in hatchery yearling Chinook salmon. *Environmental Biology of Fishes*, 96 (2-3), 135-143.

Armstrong, J. B., Schindler, D. E., Ruff, C. P., Brooks, G. T., Bentley, K. E. and Torgersen, C. E., 2013. Diel horizontal migration in streams: Juvenile fish exploit spatial heterogeneity in thermal and trophic resources. *Ecology*, 94 (9), 2066-2075.

Augspurger, J. M., Warburton, M. and Closs, G. P., 2017. Life-history plasticity in amphidromous and catadromous fishes: a continuum of strategies. *Reviews in Fish Biology and Fisheries*, 27 (1), 177-192.

Baade, U. and Fredrich, F., 1998. Movement and pattern of activity of the roach in the River Spree, Germany. *Journal of Fish Biology*, 52 (6), 1165-1174.

Backiel, T. and Zawisza, J., 1968. *Synopsis of biological data on the bream: Abramis brama (L.)*. No. 36: Food and Agriculture Organisation of the United Nations, Fish Biology Synopsis.

Baerwald, M. R., Meek, M. H., Stephens, M. R., Nagarajan, R. P., Goodbla, A. M., Tomalty, K. M., Thorgaard, G. H., May, B. and Nichols, K. M., 2016. Migration-related phenotypic divergence is associated with epigenetic modifications in rainbow trout. *Molecular Ecology*, 25 (8), 1785-1800.

Barkley, A. N., Broell, F., Pettitt-Wade, H., Watanabe, Y. Y., Marcoux, M. and Hussey, N. E., 2020. A framework to estimate the likelihood of species interactions and behavioural responses using animal-borne acoustic telemetry transceivers and accelerometers. *Journal of Animal Ecology*, 89 (1), 146-160.

Barton, K., 2020. MuMIn: Multi-Model Inference. *R package version 1.43.17*, https://CRAN.R-project.org/package=MuMIn.

BASG, 2013. *Broads Angling Strategy Group: Broads Angle*. https://www.broads.co.uk/pdf/broads-angle.pdf.

BASG, 2018. *Broads Angling Services Group* [online]. Available from: http://basgonline.org/document-library/ [Accessed 29/11/18].

Bates, D., Maechler, M., Bolker, B. and Walker, S., 2015. Fitting linear mixed-effects models using *lme4*. *Journal of Statistical Software*, 67 (1), 1-48.

Bauer, S. and Hoye, B. J., 2014. Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science*, 344 (6179), 1242552.

BBC, 2014. *Tidal surge kills thousands of fish*. Accessed 30/07/20: https://www.bbc.co.uk/news/uk-england-norfolk-29756260.

Beaudoin, C. P., Tonn, W. M., Prepas, E. E. and Wassenaar, L. I., 1999. Individual specialization and trophic adaptability of northern pike (*Esox lucius*): an isotope and dietary analysis. *Oecologia*, 120 (3), 386-396.

Bégout Anras, M., Covés, D., Dutto, G., Laffargue, P. and Lagardère, F., 2003. Tagging juvenile seabass and sole with telemetry transmitters: medium-term effects on growth. *ICES Journal of Marine Science*, 60 (6), 1328-1334.

Béguer-Pon, M., Castonguay, M., Benchetrit, J., Hatin, D., Legault, M., Verreault, G., Mailhot, Y., Tremblay, V. and Dodson, J. J., 2015. Large-scale, seasonal habitat use and movements of yellow American eels in the St. Lawrence River revealed by acoustic telemetry. *Ecology of Freshwater Fish*, 24 (1), 99-111.

Benitez, J.-P., Dierckx, A., Matondo, B. N., Rollin, X. and Ovidio, M., 2018. Movement behaviours of potamodromous fish within a large anthropised river after the reestablishment of the longitudinal connectivity. *Fisheries Research*, 207, 140-149.

Berejikian, B. A., Bush, R. A. and Campbell, L. A., 2014. Maternal control over offspring life history in a partially anadromous species, *Oncorhynchus mykiss*. *Transactions of the American Fisheries Society*, 143 (2), 369-379.

Berthold, P., 1988. Evolutionary aspects of migratory behavior in European warblers. *Journal of Evolutionary Biology*, 1 (3), 195-209.

Bertrand, M., Cabana, G., Marcogliese, D. J. and Magnan, P., 2011. Estimating the feeding range of a mobile consumer in a river–flood plain system using $\delta^{13}C$ gradients and parasites. *Journal of Animal Ecology*, 80 (6), 1313-1323.

Birnie-Gauvin, K., Højrup, L. B., Kragh, T., Jacobsen, L. and Aarestrup, K., 2019. Getting cosy in freshwater: assumed to be brackish pike are not so brackish after all. *Ecology of Freshwater Fish*, 28 (3), 376-384.

Blanchet, S., Prunier, J. G., Paz-Vinas, I., Saint-Pé, K., Rey, O., Raffard, A., Mathieu-Bégné, E., Loot, G., Fourtune, L. and Dubut, V., 2020. A river runs through it: The causes, consequences, and management of intraspecific diversity in river networks. *Evolutionary Applications*, 13, 1195-1213.

Bolland, J., Cowx, I. and Lucas, M., 2009. Evaluation of VIE and PIT tagging methods for juvenile cyprinid fishes. *Journal of Applied Ichthyology*, 25 (4), 381-386.

Bolland, J. D., Nunn, A. D., Angelopoulos, N. V., Dodd, J. R., Davies, P., Roberts, C. G., Britton, J. R. and Cowx, I. G., 2019. Refinement of acoustic-tagging protocol for twaite shad *Alosa fallax* (Lacépède), a species sensitive to handling and sedation. *Fisheries Research*, 212, 183-187.

Bond, R. M., Nicol, C. L., Kiernan, J. D. and Spence, B. C., 2019. Occurrence, fate, and confounding influence of ghost passive integrated transponder tags in an intensively monitored watershed. *Canadian Journal of Fisheries and Aquatic Sciences*, 76 (2), 286-298.

Bowen, G. J., Wassenaar, L. I. and Hobson, K. A., 2005. Global application of stable hydrogen and oxygen isotopes to wildlife forensics. *Oecologia*, 143 (3), 337-348.

Bowler, D. E. and Benton, T. G., 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological reviews,* 80 (2), 205-225.

Bradshaw, P. J., Broderick, A. C., Carreras, C., Inger, R., Fuller, W., Snape, R., Stokes, K. L. and Godley, B. J., 2017. Satellite tracking and stable isotope analysis highlight differential recruitment among foraging areas in green turtles. *Marine Ecology Progress Series*, 582, 201-214.

Braun, C. D., Skomal, G. B., Thorrold, S. R. and Berumen, M. L., 2015. Movements of the reef manta ray (*Manta alfredi*) in the Red Sea using satellite and acoustic telemetry. *Marine Biology*, 162 (12), 2351-2362.

Brennan, S. R. and Schindler, D. E., 2017. Linking otolith microchemistry and dendritic isoscapes to map heterogeneous production of fish across river basins. *Ecological Applications*, 27 (2), 363-377.

Breukelaar, A. W., Lammens, E. H., Breteler, J. G. K. and Tatrai, I., 1994. Effects of benthivorous bream (*Abramis brama*) and carp (*Cyprinus carpio*) on sediment resuspension and concentrations of nutrients and chlorophyll a. *Freshwater Biology*, 32 (1), 113-121.

Bridger, C. J. and Booth, R. K., 2003. The effects of biotelemetry transmitter presence and attachment procedures on fish physiology and behavior. *Reviews in Fisheries Science*, 11 (1), 13-34.

Britton, J. R., 2007. Reference data for evaluating the growth of common riverine fishes in the UK. *Journal of Applied Ichthyology*, 23 (5), 555-560.

Broads Authority, 2018. *Facts and figures* [online]. Available from: http://www.broads-authority.gov.uk/about-the-broads/facts-and-figures [Accessed 29/11/18].

Broads Authority, 2019. Broads Annual Water Plant Monitoring Report https://www.broads-authority.gov.uk/.

Brodersen, J., Chapman, B. B., Nilsson, P. A., Skov, C., Hansson, L.-A. and Brönmark, C., 2014. Fixed and flexible: coexistence of obligate and facultative migratory strategies in a freshwater fish. *PLoS One*, 9 (3), e90294.

Brodersen, J., Hansen, J. H. and Skov, C., 2019. Partial nomadism in large-bodied bream (*Abramis brama*). *Ecology of Freshwater Fish*, 28 (4), 650-660.

Brodersen, J., Nicolle, A., Nilsson, P. A., Skov, C., Bronmark, C. and Hansson, L. A., 2011. Interplay between temperature, fish partial migration and trophic dynamics. *Oikos*, 120 (12), 1838-1846.

Brodersen, J., Nilsson, P. A., Hansson, L.-A., Skov, C. and Brönmark, C., 2008. Condition-dependent individual decision-making determines cyprinid partial migration. *Ecology*, 89 (5), 1195-1200.

Brönmark, C., Hulthén, K., Nilsson, P. A., Skov, C., Hansson, L. A., Brodersen, J. and Chapman, B. B., 2014. There and back again: migration in freshwater fishes. *Canadian Journal of Zoology*, 92 (6), 467-479.

Brooks, J. L., Chapman, J. M., Barkley, A., Kessel, S. T., Hussey, N. E., Hinch, S. G., Patterson, D. A., Hedges, K. J., Cooke, S. J. and Fisk, A. T., 2019. Biotelemetry informing management: case studies exploring successful integration of biotelemetry data into fisheries and habitat management. *Canadian Journal of Fisheries and Aquatic Sciences*, 76 (7), 1238-1252.

Brower, L., 1996. Monarch butterfly orientation: missing pieces of a magnificent puzzle. *Journal of Experimental Biology*, 199 (1), 93-103.

Brownscombe, J. W., Griffin, L. P., Chapman, J. M., Morley, D., Acosta, A., Crossin, G. T., Iverson, S. J., Adams, A. J., Cooke, S. J. and Danylchuk, A. J., 2020. A practical method to account for variation in detection range in acoustic telemetry arrays to accurately quantify the spatial ecology of aquatic animals. *Methods in Ecology and Evolution*, 11 (1), 82-94.

Brownscombe, J. W., Lédée, E. J., Raby, G. D., Struthers, D. P., Gutowsky, L. F., Nguyen, V. M., Young, N., Stokesbury, M. J., Holbrook, C. M. and Brenden, T. O., 2019. Conducting and interpreting fish telemetry studies: considerations for researchers and resource managers. *Reviews in Fish Biology and Fisheries*, 29 (2), 369-400.

Burnham, K. P. and Anderson, D. R., 2002. *Model selection and multi-model inference: a practical information-theoretic approach*. 2nd edition. New York; London: Springer.

Busst, G. M. A. and Britton, J. R., 2018. Tissue-specific turnover rates of the nitrogen stable isotope as functions of time and growth in a cyprinid fish. *Hydrobiologia*, 805 (1), 49-60.

Cagua, E. F., Cochran, J. E., Rohner, C. A., Prebble, C. E., Sinclair-Taylor, T. H., Pierce, S. J. and Berumen, M. L., 2015. Acoustic telemetry reveals cryptic residency of whale sharks. *Biology Letters*, 11 (4), 20150092.

Campbell, H. A., Watts, M. E., Dwyer, R. G. and Franklin, C. E., 2012. V-Track: software for analysing and visualising animal movement from acoustic telemetry detections. *Marine and Freshwater Research*, 63, 815-820.

Carlson, R. E., 1977. A trophic state index for lakes. *Limnology and Oceanography*, 22 (2), 361-369.

Casselman, J. M., 1974. External sex determination of northern pike, *Esox lucius* Linnaeus. *Transactions of the American Fisheries Society*, 103 (2), 343-347.

Chapman, B., Hulthén, K., Brodersen, J., Nilsson, P. A., Skov, C., Hansson, L. A. and Brönmark, C., 2012a. Partial migration in fishes: causes and consequences. *Journal of Fish Biology*, 81 (2), 456-478.

Chapman, B., Skov, C., Hulthén, K., Brodersen, J., Nilsson, P. A., Hansson, L. A. and Brönmark, C., 2012b. Partial migration in fishes: definitions, methodologies and taxonomic distribution. *Journal of Fish Biology*, 81 (2), 479-499.

Chen, N., Krom, M. D., Wu, Y., Yu, D. and Hong, H., 2018. Storm induced estuarine turbidity maxima and controls on nutrient fluxes across river-estuary-coast continuum. *Science of the Total Environment*, 628, 1108-1120.

Childress, E. S., Allan, J. D. and McIntyre, P. B., 2014. Nutrient subsidies from iteroparous fish migrations can enhance stream productivity. *Ecosystems*, 17 (3), 522-534.

Christie, M. R. and Knowles, L. L., 2015. Habitat corridors facilitate genetic resilience irrespective of species dispersal abilities or population sizes. *Evolutionary Applications*, 8 (5), 454-463.

Clarke, K., 1990. Salt water penetration into the Upper Bure. *The Norfolk & Norwich*, 28 (5), 381.

Clément, M., Chiasson, A. G., Veinott, G. and Cairns, D. K., 2014. What otolith microchemistry and stable isotope analysis reveal and conceal about anguillid eel movements across salinity boundaries. *Oecologia*, 175 (4), 1143-1153.

Clements, S., Jepsen, D., Karnowski, M. and Schreck, C. B., 2005. Optimization of an acoustic telemetry array for detecting transmitter-implanted fish. *North American Journal of Fisheries Management*, 25 (2), 429-436.

Coffee, O., Booth, D., Thia, J. and Limpus, C., 2020. When isotopes fail: importance of satellite telemetry and multi-site validation when estimating the foraging grounds of migratory species. *Marine Ecology Progress Series*, 633, 197-206.

Cooke, S. J., Midwood, J. D., Thiem, J. D., Klimley, P., Lucas, M. C., Thorstad, E. B., Eiler, J., Holbrook, C. and Ebner, B. C., 2013. Tracking animals in freshwater with electronic tags: past, present and future. *Animal Biotelemetry*, 1 (1), 5.

Cooke, S. J., Woodley, C. M., Eppard, M. B., Brown, R. S. and Nielsen, J. L., 2011. Advancing the surgical implantation of electronic tags in fish: a gap analysis and research agenda based on a review of trends in intracoelomic tagging effects studies. *Reviews in Fish Biology and Fisheries*, 21 (1), 127-151.

Correa Ayram, C. A., Mendoza, M. E., Etter, A. and Salicrup, D. R. P., 2016. Habitat connectivity in biodiversity conservation: A review of recent studies and applications. *Progress in Physical Geography*, 40 (1), 7-37.

Courtiol, A. and Rousset, F., 2017. Modelling isoscapes using mixed models. *bioRxiv*. https://doi.org/10.1101/207662.

Courtiol, A., Rousset, F., Rohwäder, M.-S., Soto, D. X., Lehnert, L. S., Voigt, C. C., Hobson, K. A., Wassenaar, L. I. and Kramer-Schadt, S., 2019. Isoscape computation and inference of spatial origins with mixed models using the R package IsoriX. *Tracking Animal Migration with Stable Isotopes.* Elsevier, 207-236.

Cox, D. R., 1972. Regression models and life-tables. *Journal of the Royal Statistical Society: Series B (Methodological)*, 34 (2), 187-202.

Crossin, G. T., Heupel, M. R., Holbrook, C. M., Hussey, N. E., Lowerre-Barbieri, S. K., Nguyen, V. M., Raby, G. D. and Cooke, S. J., 2017. Acoustic telemetry and fisheries management. *Ecological Applications*, 27 (4), 1031-1049.

Csardi, G. and Nepusz, T., 2006. The igraph software package for complex network research. *InterJournal, Complex Systems*, 1695, http://igraph.org.

Cunjak, R., Roussel, J.-M., Gray, M., Dietrich, J., Cartwright, D., Munkittrick, K. and Jardine, T., 2005. Using stable isotope analysis with telemetry or mark-recapture data to identify fish movement and foraging. *Oecologia*, 144 (4), 636-646.

Damschen, E. I., Baker, D. V., Bohrer, G., Nathan, R., Orrock, J. L., Turner, J. R., Brudvig, L. A., Haddad, N. M., Levey, D. J. and Tewksbury, J. J., 2014. How fragmentation and corridors affect wind dynamics and seed dispersal in open habitats. *Proceedings of the National Academy of Sciences*, 111 (9), 3484-3489.

Dance, M. A., Moulton, D. L., Furey, N. B. and Rooker, J. R., 2016. Does transmitter placement or species affect detection efficiency of tagged animals in biotelemetry research? *Fisheries Research*, 183, 80-85.

Daniel, A. J., Hicks, B. J., Ling, N. and David, B. O., 2009. Acoustic and radio-transmitter retention in common carp (*Cyprinus carpio*) in New Zealand. *Marine and Freshwater Research*, 60 (4), 328-333.

Daverat, F., Limburg, K. E., Thibault, I., Shiao, J.-C., Dodson, J. J., Caron, F., Tzeng, W.-N., Iizuka, Y. and Wickström, H., 2006. Phenotypic plasticity of habitat use by three temperate eel species, *Anguilla anguilla*, *A. japonica* and *A. rostrata*. *Marine Ecology Progress Series*, 308, 231-241.

Davies, P., Britton, R. J., Nunn, A. D., Dodd, J. R., Crundwell, C., Velterop, R., Ó'Maoiléidigh, N., O'Neill, R., Sheehan, E. V. and Stamp, T., 2020. Novel insights into the marine phase and river fidelity of anadromous twaite shad *Alosa fallax* in the UK and Ireland. *Aquatic Conservation: Marine and Freshwater Ecosystems*, https://doi.org/10.1002/aqc.3343.

Debes, P. V., Piavchenko, N., Erkinaro, J. and Primmer, C. R., 2020. Genetic growth potential, rather than phenotypic size, predicts migration phenotype in Atlantic salmon. *Proceedings of the Royal Society B*, 287 (1931), 20200867.

Dekker, D., Krackhardt, D. and Snijders, T. A., 2007. Sensitivity of MRQAP tests to collinearity and autocorrelation conditions. *Psychometrika*, 72 (4), 563-581.

Delmore, K. E. and Irwin, D. E., 2014. Hybrid songbirds employ intermediate routes in a migratory divide. *Ecology Letters*, 17 (10), 1211-1218.

Deters, K. A., Brown, R. S., Carter, K. M., Boyd, J. W., Eppard, M. B. and Seaburg, A. G., 2010. Performance assessment of suture type, water temperature, and surgeon skill in juvenile Chinook salmon surgically implanted with acoustic transmitters. *Transactions of the American Fisheries Society*, 139 (3), 888-899.

Diaz Pauli, B., Wiech, M., Heino, M. and Utne-Palm, A. C., 2015. Opposite selection on behavioural types by active and passive fishing gears in a simulated guppy *Poecilia reticulata* fishery. *Journal of Fish Biology*, 86 (3), 1030-1045.

Ding, H., Zhang, Z., Xie, C., Liu, C., Chen, F., Huang, D., Li, Z., Guo, Y. and Chen, Y., 2019. An assessment of European bream *Abramis brama* (Linnaeus, 1758) fishery in the downstream of the Irtysh River in China. *Journal of Freshwater Ecology*, 34 (1), 107-122.

Dingle, H., 1996. *Migration: The Biology of Life on the Move*. New York, Oxford: Oxford University Press.

Donaldson, M. R., Hinch, S. G., Suski, C. D., Fisk, A. T., Heupel, M. R. and Cooke, S. J., 2014. Making connections in aquatic ecosystems with acoustic telemetry monitoring. *Frontiers in Ecology and the Environment*, 12 (10), 565-573.

Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z.-I., Knowler, D. J., Lévêque, C., Naiman, R. J., Prieur-Richard, A.-H., Soto, D. and Stiassny, M. L., 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews*, 81 (2), 163-182.

Duponchelle, F., Pouilly, M., Pécheyran, C., Hauser, M., Renno, J. F., Panfili, J., Darnaude, A. M., García-Vasquez, A., Carvajal-Vallejos, F. and García-Dávila, C., 2016. Trans-Amazonian natal homing in giant catfish. *Journal of Applied Ecology*, 53 (5), 1511-1520.

Dupuis-Desormeaux, M., Kaaria, T. N., Mwololo, M., Davidson, Z. and MacDonald, S. E., 2018. A ghost fence-gap: surprising wildlife usage of an obsolete fence crossing. *PeerJ*, 6, https://peerj.com/articles/5950/.

D'Urban Jackson, J., Dos Remedios, N., Maher, K. H., Zefania, S., Haig, S., Oyler-McCance, S., Blomqvist, D., Burke, T., Bruford, M. W. and Székely, T., 2017 Polygamy slows down population divergence in shorebirds. *Evolution,* 71 (5), 1313-1326.

Environment Agency, 2020a. Permit granted for next stage in Hoveton Great Broad restoration. *Press release*, https://www.gov.uk/government/news/permit-granted-for-next-stage-in-hoveton-great-broad-restoration.

Environment Agency, 2020b. *Water Qaulity Archive*. Accessed 10 June 2020: https://environment.data.gov.uk/water-quality/view/explore.

Fagan, W. F., 2002. Connectivity, fragmentation, and extinction risk in dendritic metapopulations. *Ecology*, 83 (12), 3243-3249.

Farine, D. R., 2017. A guide to null models for animal social network analysis. *Methods in Ecology and Evolution*, 8 (10), 1309-1320.

Farine, D. R., 2019. asnipe: Animal Social Network Inference and Permutations for Ecologists. *R package version 1.1.12*, https://CRAN.R-project.org/package=asnipe.

Farine, D. R. and Whitehead, H., 2015. Constructing, conducting and interpreting animal social network analysis. *Journal of Animal Ecology*, 84 (5), 1144-1163.

Faulks, L., Svanbäck, R., Eklöv, P. and Östman, Ö., 2015. Genetic and morphological divergence along the littoral–pelagic axis in two common and sympatric fishes: perch, *Perca fluviatilis* (Percidae) and roach, *Rutilus rutilus* (Cyprinidae). *Biological Journal of the Linnean Society*, 114 (4), 929-940.

Ferguson, A., Reed, T. E., Cross, T. F., McGinnity, P. and Prodöhl, P. A., 2019. Anadromy, potamodromy and residency in brown trout *Salmo trutta*: the role of genes and the environment. *Journal of Fish Biology*, 95 (3), 692-718.

Finlay, J. C. and Kendall, C., 2007. Stable isotope tracing of temporal and spatial variability in organic matter sources to freshwater ecosystems. *In:* Michener, R. and Lajtha, K., eds. *Stable Isotopes in Ecology and Environmental Science.* John Wiley & Sons, 283-333.

Flávio, H., 2020. actel: Acoustic Telemetry Data Analysis. *R package version 1.0.0.9023*, https://github.com/hugomflavio/actel.

Francis, F., 1870. *Reports on salmon ladders*. London: Horace Cox.

Franssen, N. R., Gilbert, E. I., James, A. P. and Davis, J. E., 2016. Isotopic tissue turnover and discrimination factors following a laboratory diet switch in Colorado pikeminnow (*Ptychocheilus lucius*). *Canadian Journal of Fisheries and Aquatic Sciences*, 74 (2), 265-272.

Fuchs, H., Gross, R., Stein, H. and Rottmann, O., 1998. Application of molecular genetic markers for the differentiation of bream (*Abramis brama* L.) populations from the rivers Main and Danube. *Journal of Applied Ichthyology,* 14 (1-2), 49-55.

Fullerton, A. H., Burnett, K. M., Steel, E. A., Flitcroft, R. L., Pess, G. R., Feist, B. E., Torgersen, C. E., Miller, D. J. and Sanderson, B. L., 2010. Hydrological connectivity for riverine fish: measurement challenges and research opportunities. *Freshwater Biology*, 55 (11), 2215-2237.

Gardner, C., Deeming, D. and Eady, P., 2013. Seasonal movements with shifts in lateral and longitudinal habitat use by common bream, *Abramis brama*, in a heavily modified lowland river. *Fisheries Management and Ecology*, 20 (4), 315-325.

Gardner, C., Deeming, D. C. and Eady, P., 2015a. Seasonal water level manipulation for flood risk management influences home-range size of common bream *Abramis brama* L. in a lowland river. *River Research and Applications*, 31 (2), 165-172.

Gardner, C. J., Deeming, D. C., Wellby, I., Soulsbury, C. D. and Eady, P. E., 2015b. Effects of surgically implanted tags and translocation on the movements of common bream *Abramis brama* (L.). *Fisheries Research*, 167, 252-259.

Garduno-Paz, M. V., Huntingford, F. A., Garrett, S. and Adams, C. E., 2020. A phenotypically plastic magic trait promoting reproductive isolation in sticklebacks? *Evolutionary Ecology,* 34 (1), 123-131.

German, A. V., 2019. Disturbance of synchronous oocyte development in bream *Abramis brama* L. from the Rybinsk reservoir. *Inland Water Biology,* 12 (1), 128-131.

Gillanders, B. M., 2005. Otolith chemistry to determine movements of diadromous and freshwater fish. *Aquatic Living Resources*, 18 (3), 291-300.

Gilroy, J. J., Gill, J. A., Butchart, S. H., Jones, V. R. and Franco, A. M., 2016. Migratory diversity predicts population declines in birds. *Ecology Letters*, 19 (3), 308-317.

Gjelland, K. Ø. and Hedger, R. D., 2013. Environmental influence on transmitter detection probability in biotelemetry: developing a general model of acoustic transmission. *Methods in Ecology and Evolution*, 4 (7), 665-674.

Grabowski, T. B., Thorsteinsson, V., McAdam, B. J. and Marteinsdóttir, G., 2011. Evidence of segregated spawning in a single marine fish stock: sympatric divergence of ecotypes in Icelandic cod? *PLoS One*, 6 (3), https://doi.org/10.1371/journal.pone.0017528.

Grill, G., Lehner, B., Thieme, M., Geenen, B., Tickner, D., Antonelli, F., Babu, S., Borrelli, P., Cheng, L. and Crochetiere, H., 2019. Mapping the world's free-flowing rivers. *Nature*, 569 (7755), 215-221.

Guzzo, M. M., Van Leeuwen, T. E., Hollins, J., Koeck, B., Newton, M., Webber, D. M., Smith, F. I., Bailey, D. M. and Killen, S. S., 2018. Field testing a novel high residence positioning system for monitoring the fine-scale movements of aquatic organisms. *Methods in Ecology and Evolution*, 9 (6), 1478-1488.

Hahn, L., Martins, E. G., Nunes, L. D., da Câmara, L. F., Machado, L. S. and Garrone-Neto, D., 2019. Biotelemetry reveals migratory behaviour of large catfish in the Xingu River, Eastern Amazon. *Scientific Reports*, 9 (8464), https://doi.org/10.1038/s41598-41019-44869-x.

Halfyard, E. A., Webber, D., Del Papa, J., Leadley, T., Kessel, S., Colborne, S. and Fisk, A., 2017. Evaluation of an acoustic telemetry transmitter designed to identify predation events. *Methods in Ecology and Evolution*, 8 (9), 1063-1071.

Hansen, J. H., Brodersen, J., Baktoft, H. and Skov, C., 2019a. Relationship between bream (*Abramis brama*) activity and water turbidity in a shallow lake under different season conditions. *Journal of Limnology*, 78 (2).

Hansen, J. H., Skov, C., Baktoft, H., Brönmark, C., Chapman, B. B., Hulthén, K., Hansson, L.-A., Nilsson, P. A. and Brodersen, J., 2019b. Ecological consequences of animal migration: prey partial migration affects predator ecology and prey communities. *Ecosystems*, https://doi.org/10.1007/s10021-10019-00402-10029.

Hansson, L. A., Nicolle, A., Brodersen, J., Romare, P., Nilsson, P. A., Bronmark, C. and Skov, C., 2007. Consequences of fish predation, migration, and juvenile ontogeny on zooplankton spring dynamics. *Limnology and Oceanography*, 52 (2), 696-706.

Harrington, R. R., Kennedy, B. P., Chamberlain, C. P., Blum, J. D. and Folt, C. L., 1998. ^{15}N enrichment in agricultural catchments: field patterns and applications to tracking Atlantic salmon (*Salmo salar*). *Chemical Geology*, 147 (3-4), 281-294.

Harrison, P., Gutowsky, L., Martins, E., Ward, T., Patterson, D., Cooke, S. and Power, M., 2017. Individual isotopic specializations predict subsequent inter-individual variation in movement in a freshwater fish. *Ecology*, 98 (3), 608-615.

Harrod, C., Grey, J., McCarthy, T. K. and Morrissey, M., 2005. Stable isotope analyses provide new insights into ecological plasticity in a mixohaline population of European eel. *Oecologia*, 144 (4), 673-683.

Haugen, T. O., Winfield, I. J., Vøllestad, L. A., Fletcher, J. M., James, J. B. and Stenseth, N. C., 2007. Density dependence and density independence in the demography and dispersal of pike over four decades. *Ecological Monographs*, 77 (4), 483-502.

Hayden, B., Coscia, I. and Mariani, S., 2011. Low cytochrome *b* variation in bream *Abramis brama, Journal of Fish Biology,* 78 (5), 1579-1587.

Hayden, B., Massa-Gallucci, A., Harrod, C., O'grady, M., Caffrey, J. and Kelly-Quinn, M., 2014. Trophic flexibility by roach *Rutilus rutilus* in novel habitats facilitates rapid growth and invasion success. *Journal of Fish Biology*, 84 (4), 1099-1116.

Hayden, T. A., Holbrook, C. M., Binder, T. R., Dettmers, J. M., Cooke, S. J., Vandergoot, C. S. and Krueger, C. C., 2016. Probability of acoustic transmitter detections by receiver lines in Lake Huron: results of multi-year field tests and simulations. *Animal Biotelemetry*, 4 (1), 19.

Heady, W. N. and Moore, J. W., 2013. Tissue turnover and stable isotope clocks to quantify resource shifts in anadromous rainbow trout. *Oecologia*, 172 (1), 21-34.

Helsen, K., Hermy, M. and Honnay, O., 2013. Spatial isolation slows down directional plant functional group assembly in restored semi-natural grasslands. *Journal of Applied Ecology*, 50 (2), 404-413.

Hess, J. E., Caudill, C. C., Keefer, M. L., McIlraith, B. J., Moser, M. L. and Narum, S. R., 2014. Genes predict long distance migration and large body size in a migratory fish, Pacific lamprey. *Evolutionary Applications*, 7 (10), 1192-1208.

Heupel, M., Semmens, J. M. and Hobday, A., 2006. Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. *Marine and Freshwater Research*, 57 (1), 1-13.

Heupel, M. R., Reiss, K. L., Yeiser, B. G. and Simpfendorfer, C. A., 2008. Effects of biofouling on performance of moored data logging acoustic receivers. *Limnology and Oceanography: Methods*, 6 (7), 327-335.

Heylen, B. C. and Nachtsheim, D. A., 2018. Bio-telemetry as an essential tool in movement ecology and marine conservation. *In:* Jungblut, S., Liebich, V. and Bode, M., eds. *YOUMARES 8 – Oceans Across Boundaries: Learning from each other.* Springer, Cham, 83-107.

Hindes, A., 2019. Bream spawning habitat assessment: Hoveton Great Broad and environs. *Natural England, Dragonfly House, Norwich UK*, 11 pp.

Hjelm, J., van de Weerd, G. H. and Sibbing, F. A., 2003. Functional link between foraging performance, functional morphology, and diet shift in roach (*Rutilus rutilus*). *Canadian Journal of Fisheries and Aquatic Sciences*, 60 (6), 700-709.

Hobson, K., Van Wilgenburg, S., Wassenaar, L., Powell, R., Still, C. and Craine, J., 2012. A multi-isotope ($\delta^{13}C$, $\delta^{15}N$, $\delta^{2}H$) feather isoscape to assign Afrotropical migrant birds to origins. *Ecosphere*, 3 (5), 1-20.

Hobson, K. A., Doward, K., Kardynal, K. J. and McNeil, J. N., 2018. Inferring origins of migrating insects using isoscapes: a case study using the true armyworm, *Mythimna unipuncta*, in North America. *Ecological Entomology*, 43 (3), 332-341.

Hobson, K. A. and Wassenaar, L. I., 2008. *Tracking animal migration with stable isotopes*. Academic Press.

Hodge, B. W., Wilzbach, M. A., Duffy, W. G., Quiñones, R. M. and Hobbs, J. A., 2016. Life history diversity in Klamath River steelhead. *Transactions of the American Fisheries Society*, 145 (2), 227-238.

Hodgson, J. A., Moilanen, A., Wintle, B. A. and Thomas, C. D., 2011. Habitat area, quality and connectivity: striking the balance for efficient conservation. *Journal of Applied Ecology*, 48 (1), 148-152.

Hogg, R. S., Coghlan Jr, S. M., Zydlewski, J. and Gardner, C., 2015. Fish community response to a small-stream dam removal in a Maine coastal river tributary. *Transactions of the American Fisheries Society*, 144 (3), 467-479.

Holbrook, C. M., Hayden, T., Binder, T. R. and Pye, J., 2020. glatos: A package for the Great Lakes Acoustic Telemetry Observation System. *R Package version 0.4.2*, https://gitlab.oceantrack.org/GreatLakes/glatos.

Holdway, P., Watson, R. and Moss, B., 1978. Aspects of the ecology of *Prymnesium parvum* (Haptophyta) and water chemistry in the Norfolk Broads, England. *Freshwater Biology*, 8 (4), 295-311.

How, J. R. and de Lestang, S., 2012. Acoustic tracking: issues affecting design, analysis and interpretation of data from movement studies. *Marine and Freshwater Research*, 63 (4), 312-324.

Hulthén, K., Chapman, B., Nilsson, P. A., Hansson, L. A., Skov, C., Baktoft, H., Brodersen, J. and Brönmark, C., 2014. Sex identification and PIT-tagging: tools and prospects for studying intersexual differences in freshwater fishes. *Journal of Fish Biology*, 84 (2), 503-512.

Humphries, P. and Winemiller, K. O., 2009. Historical impacts on river fauna, shifting baselines, and challenges for restoration. *BioScience*, 59 (8), 673-684.

Hurvich, C. M., Simonoff, J. S. and Tsai, C. L., 1998. Smoothing parameter selection in nonparametric regression using an improved Akaike information criterion. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, 60 (2), 271-293.

Hussey, N. E., Kessel, S. T., Aarestrup, K., Cooke, S. J., Cowley, P. D., Fisk, A. T., Harcourt, R. G., Holland, K. N., Iverson, S. J. and Kocik, J. F., 2015. Aquatic animal telemetry: a panoramic window into the underwater world. *Science*, 348 (6240), 1255642.

Huveneers, C., Simpfendorfer, C. A., Kim, S., Semmens, J. M., Hobday, A. J., Pederson, H., Stieglitz, T., Vallee, R., Webber, D. and Heupel, M. R., 2016. The influence of environmental parameters on the performance and detection range of acoustic receivers. *Methods in Ecology and Evolution*, 7 (7), 825-835.

Ibarz, A., Ordóñez-Grande, B., Sanahuja, I., Sánchez-Nuño, S., Fernández-Borràs, J., Blasco, J. and Fernández-Alacid, L., 2019. Using stable isotope analysis to study skin mucus exudation and renewal in fish. *Journal of Experimental Biology*, 222 (8), jeb 195925.

ITV, 2015. *Toxic algae killing thousands of fish on the Norfolk Broads*. https://www.itv.com/news/anglia/2015-04-15/toxic-algae-killing-thousands-of-fish-on-the-norfolk-broads. [Accessed 30/09/2020]

Jackson, A. L., Inger, R., Parnell, A. C. and Bearhop, S., 2011. Comparing isotopic niche widths among and within communities: SIBER–Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology*, 80 (3), 595-602.

Jackson, C. H., 2011. Multi-state models for panel data: the msm package for R. *Journal of Statistical Software*, 38 (8), 1-29.

Jacobsen, L., Bekkevold, D., Berg, S., Jepsen, N., Koed, A., Aarestrup, K., Baktoft, H. and Skov, C., 2017. Pike (*Esox lucius* L.) on the edge: consistent individual movement patterns in transitional waters of the western Baltic. *Hydrobiologia*, 784 (1), 143-154.

Jacoby, D. M., Casselman, J. M., Crook, V., DeLucia, M.-B., Ahn, H., Kaifu, K., Kurwie, T., Sasal, P., Silfvergrip, A. M. and Smith, K. G., 2015. Synergistic patterns of threat and the challenges facing global anguillid eel conservation. *Global Ecology and Conservation*, 4, 321-333.

Jaeger, A., Lecomte, V. J., Weimerskirch, H., Richard, P. and Cherel, Y., 2010. Seabird satellite tracking validates the use of latitudinal isoscapes to depict predators' foraging areas in the Southern Ocean. *Rapid Communications in Mass Spectrometry*, 24 (23), 3456-3460.

Jepsen, N. and Aarestrup, K., 1999. A comparison of the growth of radio-tagged and dye-marked pike. *Journal of Fish Biology*, 55 (4), 880-883.

Jepsen, N., Koed, A., Thorstad, E. B. and Baras, E., 2002. Surgical implantation of telemetry transmitters in fish: how much have we learned? *Aquatic Telemetry*. Springer, 239-248.

Jepsen, N., Pedersen, S. and Thorstad, E., 2000. Behavioural interactions between prey (trout smolts) and predators (pike and pikeperch) in an impounded river. *Regulated Rivers: Research & Management*, 16 (2), 189-198.

Jepsen, N., Schreck, C., Clements, S. and Thorstad, E., 2003. A brief discussion on the 2% tag/bodymass rule of thumb. *In:* Spedicato, M., Lembo, G. and Marmulla, G., eds. *Aquatic telemetry: advances and applications. Proceedings of the Fifth Conference on Fish Telemetry.* Rome, 255-259.

Jones, J., Börger, L., Tummers, J., Jones, P., Lucas, M., Kerr, J., Kemp, P., Bizzi, S., Consuegra, S. and Marcello, L., 2019. A comprehensive assessment of stream fragmentation in Great Britain. *Science of the Total Environment*, 673, 756-762.

Jordan, D. and Wortley, J., 1985. Sampling strategy related to fish distribution, with particular reference to the Norfolk Broads. *Journal of Fish Biology*, 27, 163-173.

Jorgensen, S. J., Reeb, C. A., Chapple, T. K., Anderson, S., Perle, C., Van Sommeran, S. R., Fritz-Cope, C., Brown, A. C., Klimley, A. P. and Block, B. A., 2010. Philopatry and migration of Pacific white sharks. *Proceedings of the Royal Society B: Biological Sciences*, 277, 679-688.

Jousimo, J., Tack, A. J., Ovaskainen, O., Mononen, T., Susi, H., Tollenaere, C. and Laine, A.-L., 2014. Ecological and evolutionary effects of fragmentation on infectious disease dynamics. *Science*, 344 (6189), 1289-1293.

Jurajda, P., Adámek, Z., Janáč, M., Roche, K., Mikl, L., Rederer, L., Zapletal, T., Koza, V. and Špaček, J., 2016. Use of multiple fish-removal methods during biomanipulation of a drinking water reservoir–evaluation of the first four years. *Fisheries Research*, 173, 101-108.

Kafemann, R., Adlerstein, S. and Neukamm, R., 2000. Variation in otolith strontium and calcium ratios as an indicator of life-history strategies of freshwater fish species within a brackish water system. *Fisheries Research*, 46 (1-3), 313-325.

Kärgenberg, E., Økland, F., Thalfeldt, M., Thorstad, E. B., Sandlund, O. T. and Tambets, M., 2020. Migration patterns of a potamodromous piscivore, asp (*Leuciscus aspius*), in a river-lake system. *Journal of Fish Biology*, https://doi.org/10.1111/jfb.14454.

Kennedy, B. P., Chamberlain, C. P., Blum, J. D., Nislow, K. H. and Folt, C. L., 2005. Comparing naturally occurring stable isotopes of nitrogen, carbon, and strontium as markers for the rearing locations of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, 62 (1), 48-57.

Kennedy, M. and Fitzmaurice, P., 1968. The biology of the bream *Abramis Brama* (L) in Irish waters, *Proceedings of the Royal Irish Academy* (pp. 95-157): Inland Fisheries Trust, Dublin.

Kerr, L. A. and Secor, D. H., 2012. Partial migration across populations of white perch (*Morone americana*): a flexible life history strategy in a variable estuarine environment. *Estuaries and Coasts*, 35 (1), 227-236.

Kerr, L. A., Secor, D. H. and Piccoli, P. M., 2009. Partial migration of fishes as exemplified by the estuarine-dependent white perch. *Fisheries,* 34 (3), 114-123.

Kessel, S., Chapman, D., Franks, B., Gedamke, T., Gruber, S., Newman, J., White, E. and Perkins, R. G., 2014a. Predictable temperature-regulated residency, movement and migration in a large, highly mobile marine predator (*Negaprion brevirostris*). *Marine Ecology Progress Series*, 514, 175-190.

Kessel, S., Cooke, S., Heupel, M., Hussey, N., Simpfendorfer, C., Vagle, S. and Fisk, A., 2014b. A review of detection range testing in aquatic passive acoustic telemetry studies. *Reviews in Fish Biology and Fisheries*, 24 (1), 199-218.

Kessel, S., Hussey, N., Crawford, R., Yurkowski, D., O'Neill, C. and Fisk, A., 2016. Distinct patterns of Arctic cod (*Boreogadus saida*) presence and absence in a shallow high Arctic embayment, revealed across open-water and ice-covered periods through acoustic telemetry. *Polar Biology*, 39 (6), 1057-1068.

Kessel, S. T., Hondorp, D. W., Holbrook, C. M., Boase, J. C., Chiotti, J. A., Thomas, M. V., Wills, T. C., Roseman, E. F., Drouin, R. and Krueger, C. C., 2018. Divergent migration within lake sturgeon (*Acipenser fulvescens*) populations: Multiple distinct patterns exist across an unrestricted migration corridor. *Journal of Animal Ecology*, 87 (1), 259-273.

Killen, S. S., Marras, S., Nadler, L. and Domenici, P., 2017. The role of physiological traits in assortment among and within fish shoals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372, 20160233.

Kipling, C. and Frost, W. E., 1970. A study of the mortality, population numbers, year class strengths, production and food consumption of pike, *Esox lucius* L., in Windermere from 1944 to 1962. *The Journal of Animal Ecology*, 115-157.

Klemetsen, A., Amundsen, P. A., Dempson, J., Jonsson, B., Jonsson, N., O'connell, M. and Mortensen, E., 2003. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecology of Freshwater Fish*, 12 (1), 1-59.

Klimley, A. P., Voegeli, F., Beavers, S. C. and Le Boeuf, B. J., 1998. Automated listening stations for tagged marine fishes. *Marine Technology Society Journal*, 32 (1), 94-101.

Klinard, N. V., Halfyard, E. A., Fisk, A. T., Stewart, T. J. and Johnson, T. B., 2018. Effects of surgically implanted acoustic tags on body condition, growth, and survival in a small, laterally compressed forage fish. *Transactions of the American Fisheries Society*, 147 (4), 749-757.

Klinard, N. V., Halfyard, E. A., Matley, J. K., Fisk, A. T. and Johnson, T. B., 2019a. The influence of dynamic environmental interactions on detection efficiency of acoustic transmitters in a large, deep, freshwater lake. *Animal Biotelemetry*, 7 (1), 17.

Klinard, N. V. and Matley, J. K., 2020. Living until proven dead: addressing mortality in acoustic telemetry research. *Reviews in Fish Biology and Fisheries*, https://doi.org/10.1007/s11160-11020-09613-z.

Klinard, N. V., Matley, J. K., Fisk, A. T. and Johnson, T. B., 2019b. Long-term retention of acoustic telemetry transmitters in temperate predators revealed by predation tags implanted in wild prey fish. *Journal of Fish Biology*, 95 (6), 1512-1516.

Klinga, P., Mikoláš, M., Smolko, P., Tejkal, M., Höglund, J. and Paule, L., 2019. Considering landscape connectivity and gene flow in the Anthropocene using complementary landscape genetics and habitat modelling approaches. *Landscape Ecology*, 34 (3), 521-536.

Koed, A., Balleby, K., Mejlhede, P. and Aarestrup, K., 2006. Annual movement of adult pike (*Esox lucius* L.) in a lowland river. *Ecology of Freshwater Fish*, 15 (2), 191-199.

Kompowski, A., 1988. Growth rate of bream, *Abramis brama* (L., 1758), in lake Dabie and the Szczecin lagoon. *Acta Ichthyologica et Piscatoria*, 18, 35-48.

Koper, N. and Manseau, M., 2009. Generalized estimating equations and generalized linear mixed-effects models for modelling resource selection. *Journal of Applied Ecology*, 46 (3), 590-599.

Krams, I. A., Rumvolt, K., Saks, L., Krams, R., Elferts, D., Vrublevska, J., Rantala, M. J., Kecko, S., Cīrule, D. and Luoto, S., 2017. Reproduction compromises adaptive immunity in a cyprinid fish. *Ecological Research*, 32 (4), 559-566.

Larsen, T., Hansen, T. and Dierking, J., 2020. Characterizing niche differentiation among marine consumers with amino acid $\delta^{13}C$ fingerprinting. *Ecology and Evolution*, 10 (14), 7768-7782.

Larsen, T., Yokoyama, Y. and Fernandes, R., 2018. Radiocarbon in ecology: Insights and perspectives from aquatic and terrestrial studies. *Methods in Ecology and Evolution*, 9 (1), 181-190.

Le Pichon, C., Coustillas, J., Zahm, A., Bunel, M., Gazeau-Nadin, C. and Rochard, E., 2017. Summer use of the tidal freshwaters of the River Seine by three estuarine fish: Coupling telemetry and GIS spatial analysis. *Estuarine, Coastal and Shelf Science*, 196, 83-96.

Leander, J., Klaminder, J., Jonsson, M., Brodin, T., Leonardsson, K. and Hellström, G., 2020. The old and the new: evaluating performance of acoustic telemetry systems in tracking migrating Atlantic salmon (*Salmo salar*) smolt and European eel (*Anguilla anguilla*) around hydropower facilities. *Canadian Journal of Fisheries and Aquatic Sciences*, 77 (1), 177-187.

Lennox, R. J., Paukert, C. P., Aarestrup, K., Auger-Méthé, M., Baumgartner, L., Birnie-Gauvin, K., Bøe, K., Brink, K., Brownscombe, J. W., Chen, Y., Davidsen, J. G., Eliason, E. J., Filous, A., Gillanders, B. M., Helland, I. P., Horodysky, A. Z., Januchowski-Hartley, S. R., Lowerre-Barbieri, S. K., Lucas, M. C., Martins, E. G., Murchie, K. J., Pompeu, P. S., Power, M., Raghavan, R., Rahel, F. J., Secor, D., Thiem, J. D., Thorstad, E. B., Ueda, H., Whoriskey, F. G. and Cooke, S. J., 2019. One hundred pressing questions on the future of global fish migration science, conservation, and policy. *Frontiers in Ecology and Evolution*, 7, 286.

Leuven, R. S., van der Velde, G., Baijens, I., Snijders, J., van der Zwart, C., Lenders, H. R. and bij de Vaate, A., 2009. The river Rhine: a global highway for dispersal of aquatic invasive species. *Biological Invasions*, 11 (9), 1989.

Lidgard, D. C., Bowen, W. D., Jonsen, I. D. and Iverson, S. J., 2012. Animal-borne acoustic transceivers reveal patterns of at-sea associations in an upper-trophic level predator. *PloS One*, 7 (11), e48962.

Liu, X. and Wang, H., 2010. Estimation of minimum area requirement of river-connected lakes for fish diversity conservation in the Yangtze River floodplain. *Diversity and Distributions*, 16 (6), 932-940.

Loehle, C. and Eschenbach, W., 2012. Historical bird and terrestrial mammal extinction rates and causes. *Diversity and Distributions*, 18 (1), 84-91.

Louison, M. J., Jeffrey, J. D., Suski, C. D. and Stein, J. A., 2018. Sociable bluegill, *Lepomis macrochirus*, are selectively captured via recreational angling. *Animal Behaviour*, 142, 129-137.

Lucas, M., Thom, T., Duncan, A. and Slavik, O., 1998. *Coarse Fish Migration Occurrence, Causes and Implications: Technical Report*. Environment Agency.

Lucas, M. C. and Baras, E., 2000. Methods for studying spatial behaviour of freshwater fishes in the natural environment. *Fish and Fisheries*, 1 (4), 283-316.

Lucas, M. C. and Baras, E., 2001. *Migration of Freshwater Fishes*. Malden, MA: Blackwell Science.

Lucas, M. C., Bubb, D. H., Jang, M. H., Ha, K. and Masters, J. E., 2009. Availability of and access to critical habitats in regulated rivers: effects of low-head barriers on threatened lampreys. *Freshwater Biology*, 54 (3), 621-634.

Lyons, J. and Lucas, M., 2002. The combined use of acoustic tracking and echosounding to investigate the movement and distribution of common bream (*Abramis brama*) in the River Trent, England. *Hydrobiologia*, 483 (1-3), 265-273.

MacArthur, R. H. and Wilson, E. O., 1967. *The Theory of Island Biogeography*. Princeton: Princeton University Press.

MacCall, A. D., Francis, T. B., Punt, A. E., Siple, M. C., Armitage, D. R., Cleary, J. S., Dressel, S. C., Jones, R. R., Kitka, H. and Lee, L. C., 2019. A heuristic model of socially learned migration behaviour exhibits distinctive spatial and reproductive dynamics. *ICES Journal of Marine Science*, 76 (2), 598-608.

Magilligan, F. J., Graber, B. E., Nislow, K. H., Chipman, J. W., Sneddon, C. S. and Fox, C. A., 2016. River restoration by dam removal: Enhancing connectivity at watershed scales. *Elementa: Science of the Anthropocene*, 4, http://doi.org/10.12952/journal.elementa.000108.

Marty, G. D. and Summerfelt, R. C., 1986. Pathways and mechanisms for expulsion of surgically implanted dummy transmitters from channel catfish. *Transactions of the American Fisheries Society*, 115 (4), 577-589.

Massol, F., Gravel, D., Mouquet, N., Cadotte, M. W., Fukami, T. and Leibold, M. A., 2011. Linking community and ecosystem dynamics through spatial ecology. *Ecology Letters*, 14 (3), 313-323.

Matérn, B., 1960. *Spatial variation*. Vol. 36. Springer Science & Business Media.

Mathies, N. H., Ogburn, M. B., McFall, G. and Fangman, S., 2014. Environmental interference factors affecting detection range in acoustic telemetry studies using fixed receiver arrays. *Marine Ecology Progress Series*, 495, 27-38.

Matsubayashi, J., Osada, Y., Tadokoro, K., Abe, Y., Yamaguchi, A., Shirai, K., Honda, K., Yoshikawa, C., Ogawa, N. O. and Ohkouchi, N., 2020. Tracking long-distance migration of marine fishes using compound-specific stable isotope analysis of amino acids. *Ecology Letters*, 23 (5), 881-890.

Mayor, S. J., Schneider, D. C., Schaefer, J. A. and Mahoney, S. P., 2009. Habitat selection at multiple scales. *Ecoscience*, 16 (2), 238-247.

McMahon, K. W. and Newsome, S. D., 2019. Amino acid isotope analysis: a new frontier in studies of animal migration and foraging ecology. *In:* Hobson, K. A. and Wassenaar, L. I., eds. *Tracking Animal Migration With Stable Isotopes.* Elsevier, 173-190.

McMichael, G. A., Eppard, M. B., Carlson, T. J., Carter, J. A., Ebberts, B. D., Brown, R. S., Weiland, M., Ploskey, G. R., Harnish, R. A. and Deng, Z. D., 2010. The juvenile salmon acoustic telemetry system: a new tool. *Fisheries*, 35 (1), 9-22.

Medwin, H. and Clay, C. S., 1998. *Fundamentals of acoustical oceanography*. Amsterdam: Elsevier Science.

Molls, F., 1999. New insights into the migration and habitat use by bream and white bream in the floodplain of the River Rhine. *Journal of Fish Biology*, 55 (6), 1187-1200.

Montorio, L., Evanno, G. and Nevoux, M., 2018. Intra-and interspecific densities shape life-history traits in a salmonid population. *Oecologia*, 188 (2), 451-464.

Moore, A., Russell, I. and Potter, E., 1990. The effects of intraperitoneally implanted dummy acoustic transmitters on the behaviour and physiology of juvenile Atlantic salmon, *Salmo salar* L. *Journal of Fish Biology*, 37 (5), 713-721.

Morgan, M. and Trippel, E., 1996. Skewed sex ratios in spawning shoals of Atlantic cod (*Gadus morhua)*. *ICES Journal of Marine Science*, 53 (5), 820-826.

Moss, B., 1977. Conservation problems in the Norfolk Broads and rivers of East Anglia, England—phytoplankton, boats and the causes of turbidity. *Biological Conservation*, 12 (2), 95-114.

Moss, B. and Balls, H., 1989. Phytoplankton distribution in a floodplain lake and river system. II Seasonal changes in the phytoplankton communities and their control by hydrology and nutrient availability. *Journal of Plankton Research*, 11 (4), 839-867.

Moss, B., Stansfield, J., Irvine, K., Perrow, M. and Phillips, G., 1996. Progressive restoration of a shallow lake: a 12-year experiment in isolation, sediment removal and biomanipulation. *Journal of Applied Ecology*, 33, 71-86.

Murray, D. L., 2006. On improving telemetry-based survival estimation. *The Journal of Wildlife Management*, 70 (6), 1530-1543.

Natural England, 2020. *Designated Sites View*. https://designatedsites.naturalengland.org.uk/ [Accessed on 23/07/20.]

Neves, V., Silva, D., Martinho, F., Antunes, C., Ramos, S. and Freitas, V., 2018. Assessing the effects of internal and external acoustic tagging methods on European flounder *Platichthys flesus*. *Fisheries Research*, 206, 202-208.

Newcomer Johnson, T. A., Kaushal, S. S., Mayer, P. M., Smith, R. M. and Sivirichi, G. M., 2016. Nutrient retention in restored streams and rivers: A global review and synthesis. *Water*, 8 (4), 116.

Newton, M., Barry, J., Dodd, J. A., Lucas, M. C., Boylan, P. and Adams, C. E., 2016. Does size matter? A test of size-specific mortality in Atlantic salmon *Salmo salar* smolts tagged with acoustic transmitters. *Journal of Fish Biology*, 89 (3), 1641-1650.

Nislow, K. H., Hudy, M., Letcher, B. H. and Smith, E. P., 2011. Variation in local abundance and species richness of stream fishes in relation to dispersal barriers: implications for management and conservation. *Freshwater Biology*, 56 (10), 2135-2144.

Noonan, M. J., Grant, J. W. and Jackson, C. D., 2012. A quantitative assessment of fish passage efficiency. *Fish and Fisheries*, 13 (4), 450-464.

Olds, A. D., Connolly, R. M., Pitt, K. A., Pittman, S. J., Maxwell, P. S., Huijbers, C. M., Moore, B. R., Albert, S., Rissik, D. and Babcock, R. C., 2016. Quantifying the conservation value of seascape connectivity: a global synthesis. *Global Ecology and Biogeography*, 25 (1), 3-15.

Oskarsson, G. J., Gudmundsdottir, A. and Sigurdsson, T., 2009. Variation in spatial distribution and migration of Icelandic summer-spawning herring. *ICES Journal of Marine Science*, 66 (8), 1762-1767.

Pallis, M., 1911. On the cause of the salinity of the Broads of the River Thurne. *The Geographical Journal*, 37 (3), 284-291.

Pander, J., Mueller, M. and Geist, J., 2018. Habitat diversity and connectivity govern the conservation value of restored aquatic floodplain habitats. *Biological Conservation*, 217, 1-10.

Pärssinen, V., Hulthén, K., Brönmark, C., Skov, C., Brodersen, J., Baktoft, H., Chapman, B. B., Hansson, L. A. and Anders Anders Nilsson, P., 2020. Maladaptive migration behaviour in hybrids links to predator-mediated ecological selection. *Journal of Animal Ecology*, DOI: 10.1111/1365-2656.13308.

Pauwels, I. S., Goethals, P., Coeck, J. and Mouton, A., 2017. Habitat use and preference of adult pike (*Esox lucius* L.) in an anthropogenically impacted lowland river. *Limnologica*, 62, 151-160.

Payne, N. L., Gillanders, B. M., Webber, D. M. and Semmens, J. M., 2010. Interpreting diel activity patterns from acoustic telemetry: the need for controls. *Marine Ecology Progress Series*, 419, 295-301.

Pearson, R. M., Van De Merwe, J. P., Gagan, M. K. and Connolly, R. M., 2020. Unique post-telemetry recapture enables development of multi-element isoscapes from barnacle shell for retracing host movement. *Frontiers in Marine Science*, 7, 596.

Perga, M. and Gerdeaux, D., 2005. 'Are fish what they eat' all year round? *Oecologia*, 144 (4), 598-606.

Perrow, M., Jowitt, A., Leigh, S., Hindes, A. and Rhodes, J., 1999. The stability of fish communities in shallow lakes undergoing restoration: expectations and experiences from the Norfolk Broads (UK). *Hydrobiologia*, 408/409, 85-100.

Persson, A. and Brönmark, C., 2002. Foraging capacities and effects of competitive release on ontogenetic diet shift in bream, *Abramis brama*. *Oikos*, 97 (2), 271-281.

Pess, G., Quinn, T., Gephard, S. R. and Saunders, R., 2014. Re-colonization of Atlantic and Pacific rivers by anadromous fishes: linkages between life history and the benefits of barrier removal. *Reviews in Fish Biology and Fisheries*, 24 (3), 881-900.

Peterson, B. J. and Fry, B., 1987. Stable isotopes in ecosystem studies. *Annual review of ecology and systematics*, 18 (1), 293-320.

Phillips, G. and Jackson, R., 1990. The control of eutrophication in very shallow lakes, the Norfolk Broads. *Verhandlungen des Internationalen Verein Limnologie*, 24 (1), 573-575.

Pickett, S. T. A. and White, P. S., 1985. *The ecology of natural disturbance and patch dynamics*. Orlando, FL: Academic Press.

Pincock, D. G., 2012. False detections: what they are and how to remove them from detection data. *Vemco Application Note*, DOC-004691-03, http://vemco.com/wp-content/uploads/2012/2011/false_detections.pdf.

Pinder, L., 1997. Research on the Great Ouse: overview and implications for management. *Regulated Rivers: Research & Management*, 13 (3), 309-315.

Pomilla, C. and Rosenbaum, H. C., 2005. Against the current: an inter-oceanic whale migration event. *Biology Letters*, 1 (4), 476-479.

Poncin, P., Matondo, B. N., Termol, C., Kestemont, P. and Philippart, J.-C., 2011. Relationships between circulating androgens, aggressive behaviour and breeding tubercles in males of the common bream *Abramis brama* L. in an aquarium environment. *Fish Physiology and Biochemistry*, 37 (3), 533-542.

Post, D. M., 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology*, 83 (3), 703-718.

Quinn, T. P., Bond, M. and Slater, S., 2014. Use of stable isotopes and otolith micro-chemistry to evaluate migration in male chinook salmon, *Oncorhynchus tshawytscha*, from an Alaskan river. *Northwest Science*, 88 (4), 360-366.

R Core Team, 2019. *R: A language and environment for statistical computing* [online]. Vienna, Austria: R Foundation for Statistical Computing. Available from: https://www.R-project.org/

R Core Team, 2020. *R: A language and environment for statistical computing* [online]. Vienna, Austria: R Foundation for Statistical Computing. Available from: https://www.R-project.org/

Radinger, J., Britton, J. R., Carlson, S. M., Magurran, A. E., Alcaraz-Hernández, J. D., Almodóvar, A., Benejam, L., Fernández-Delgado, C., Nicola, G. G. and Oliva-Paterna, F. J., 2019. Effective monitoring of freshwater fish. *Fish and Fisheries*, 20 (4), 729-747.

Rahel, F. J., 2013. Intentional fragmentation as a management strategy in aquatic systems. *BioScience*, 63 (5), 362-372.

Rahel, F. J. and McLaughlin, R. L., 2018. Selective fragmentation and the management of fish movement across anthropogenic barriers. *Ecological Applications*, 28 (8), 2066-2081.

Rasmussen, J. B., Trudeau, V. and Morinville, G., 2009. Estimating the scale of fish feeding movements in rivers using $\delta^{13}C$ signature gradients. *Journal of Animal Ecology*, 78 (3), 674-685.

Raspisaniye Pogodi Ltd, 2020. *https://rp5.ru/docs/about/en*. [Accessed 06/05/2020].

Reid, A. J., Carlson, A. K., Creed, I. F., Eliason, E. J., Gell, P. A., Johnson, P. T., Kidd, K. A., MacCormack, T. J., Olden, J. D. and Ormerod, S. J., 2019. Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biological Reviews*, 94 (3), 849-873.

Reubens, J., Verhelst, P., van der Knaap, I., Deneudt, K., Moens, T. and Hernandez, F., 2019. Environmental factors influence the detection probability in acoustic telemetry in a marine environment: results from a new setup. *Hydrobiologia*, 845 (1), 81-94.

Richards, S. A., Whittingham, M. J. and Stephens, P. A., 2011. Model selection and model averaging in behavioural ecology: the utility of the IT-AIC framework. *Behavioral Ecology and Sociobiology*, 65 (1), 77-89.

Robichaud, D. and Rose, G. A., 2004. Migratory behaviour and range in Atlantic cod: inference from a century of tagging. *Fish and Fisheries*, 5 (3), 185-214.

Rodger, J. R., Honkanen, H. M., Bradley, C. R., Boylan, P., Prodöhl, P. A. and Adams, C. E., 2020. Genetic structuring across alternative life-history tactics and small spatial scales in brown trout (*Salmo trutta*). *Ecology of Freshwater Fish*, DOI: 10.1111/eff.12573.

Rub, A. M. W. and Sandford, B. P., 2020. Evidence of a 'dinner bell'effect from acoustic transmitters in adult Chinook salmon. *Marine Ecology Progress Series*, 641, 1-11.

Ruiz-Navarro, A., Gillingham, P. K. and Britton, J. R., 2016. Shifts in the climate space of temperate cyprinid fishes due to climate change are coupled with altered body sizes and growth rates. *Global Change Biology*, 22 (9), 3221-3232.

Ryser, R., Häussler, J., Stark, M., Brose, U., Rall, B. C. and Guill, C., 2019. The biggest losers: Habitat isolation deconstructs complex food webs from top to bottom. *Proceedings of the Royal Society B*, 286, 20191177.

Saitoh, Y., Nakano, T., Shin, K. C., Matsubayashi, J., Kato, Y., Amakawa, H., Osada, Y., Yoshimizu, C., Okuda, N. and Amano, Y., 2018. Utility of Nd isotope ratio as a tracer of marine animals: regional variation in coastal seas and causal factors. *Ecosphere*, 9 (8), e02365.

Schindler, D. E., Hilborn, R., Chasco, B., Boatright, C. P., Quinn, T. P., Rogers, L. A. and Webster, M. S., 2010. Population diversity and the portfolio effect in an exploited species. *Nature*, 465 (7298), 609-612.

Schoonyan, A., Kraus, R. T., Faust, M. D., Vandergoot, C. S., Cooke, S. J., Cook, H. A., Hayden, T. A. and Krueger, C. C., 2017. Estimating incision healing rate for surgically implanted acoustic transmitters from recaptured fish. *Animal Biotelemetry*, 5 (1), 1-8.

Schulz, U. and Berg, R., 1987. The migration of ultrasonic-tagged bream, *Abramis brama* (L), in Lake Constance (Bodensee-Untersee). *Journal of Fish Biology*, 31 (3), 409-414.

Selby, T. H., Hart, K. M., Fujisaki, I., Smith, B. J., Pollock, C. J., Hillis-Starr, Z., Lundgren, I. and Oli, M. K., 2016. Can you hear me now? Range-testing a submerged passive acoustic receiver array in a Caribbean coral reef habitat. *Ecology and Evolution*, 6 (14), 4823-4835.

Seminoff, J. A., Benson, S. R., Arthur, K. E., Eguchi, T., Dutton, P. H., Tapilatu, R. F. and Popp, B. N., 2012. Stable isotope tracking of endangered sea turtles: validation with satellite telemetry and $\delta^{15}N$ analysis of amino acids. *PLoS One*, 7 (5).

Semizer-Cuming, D., Kjær, E. D. and Finkeldey, R., 2017. Gene flow of common ash (Fraxinus excelsior L.) in a fragmented landscape. *PloS One*, 12 (10), e0186757.

Shepherd, B. and Whittington, J., 2006. Response of wolves to corridor restoration and human use management. *Ecology and Society*, 11 (2), https://www.ecologyandsociety.org/vol11/iss12/art11/main.html.

Shroyer, S. M. and Logsdon, D. E., 2009. Detection distances of selected radio and acoustic tags in Minnesota lakes and rivers. *North American Journal of Fisheries Management*, 29 (4), 876-884.

Silva, A. T., Lucas, M. C., Castro-Santos, T., Katopodis, C., Baumgartner, L. J., Thiem, J. D., Aarestrup, K., Pompeu, P. S., O'Brien, G. C. and Braun, D. C., 2018. The future of fish passage science, engineering, and practice. *Fish and Fisheries*, 19 (2), 340-362.

Simmons, O. M., Britton, J. R., Gillingham, P. K. and Gregory, S. D., 2020. Influence of environmental and biological factors on the overwinter growth rate of Atlantic salmon *Salmo salar* parr in a UK chalk stream. *Ecology of Freshwater Fish*, https://doi.org/10.1111/eff.12542.

Simpfendorfer, C. A., Heupel, M. R. and Collins, A. B., 2008. Variation in the performance of acoustic receivers and its implication for positioning algorithms in a riverine setting. *Canadian Journal of Fisheries and Aquatic Sciences*, 65 (3), 482-492.

Simpfendorfer, C. A., Huveneers, C., Steckenreuter, A., Tattersall, K., Hoenner, X., Harcourt, R. and Heupel, M. R., 2015. Ghosts in the data: false detections in VEMCO pulse position modulation acoustic telemetry monitoring equipment. *Animal Biotelemetry*, 3 (1), 55.

Skov, C., Baktoft, H., Brodersen, J., Brönmark, C., Chapman, B. B., Hansson, L.-A. and Nilsson, P. A., 2011. Sizing up your enemy: individual predation vulnerability predicts migratory probability. *Proceedings of the Royal Society B: Biological Sciences*, 278 (1710), 1414-1418.

Skov, C., Brodersen, J., Brönmark, C., Hansson, L. A., Hertonsson, P. and Nilsson, P., 2005. Evaluation of PIT-tagging in cyprinids. *Journal of Fish Biology*, 67 (5), 1195-1201.

Skov, C., Hansen, J. H., Baktoft, H., Brönmark, C., Brodersen, J., Chapman, B. B., Hansson, L. A., Hulthén, K. and Nilsson, P. A., 2020. A field evaluation of long-term effects of PIT tagging. *Journal of Fish Biology*, 96 (4), 1055-1059.

Šmejkal, M., Bartoň, D., Děd, V., Souza, A. T., Blabolil, P., Vejřík, L., Sajdlová, Z., Říha, M. and Kubečka, J., 2020. Negative feedback concept in tagging: Ghost tags imperil the long-term monitoring of fishes. *Plos One*, 15 (3), e0229350.

Šmejkal, M., Blabolil, P., Bartoň, D., Duras, J., Vejřík, L., Sajdlová, Z., Kočvara, L. and Kubečka, J., 2019. Sex-specific probability of PIT tag retention in a cyprinid fish. *Fisheries Research*, 219, 105325.

Søndergaard, M., Liboriussen, L., Pedersen, A. R. and Jeppesen, E., 2008. Lake restoration by fish removal: short-and long-term effects in 36 Danish lakes. *Ecosystems*, 11 (8), 1291-1305.

Stakėnas, S., Copp, G. and Scott, D., 2009. Tagging effects on three non-native fish species in England (*Lepomis gibbosus, Pseudorasbora parva, Sander lucioperca*) and of native *Salmo trutta*. *Ecology of Freshwater Fish*, 18 (2), 167-176.

Stasko, A. and Pincock, D., 1977. Review of underwater biotelemetry, with emphasis on ultrasonic techniques. *Journal of the Fisheries Board of Canada*, 34 (9), 1261-1285.

Strange, R. J., Schreck, C. B. and Golden, J. T., 1977. Corticoid stress responses to handling and temperature in salmonids. *Transactions of the American Fisheries Society*, 106 (3), 213-218.

Suzuki, K. W., Kasai, A., Nakayama, K. and Tanaka, M., 2005. Differential isotopic enrichment and half-life among tissues in Japanese temperate bass (*Lateolabrax japonicus*) juveniles: implications for analyzing migration. *Canadian Journal of Fisheries and Aquatic Sciences*, 62 (3), 671-678.

Takekawa, J. Y., Ackerman, J. T., Brand, L. A., Graham, T. R., Eagles-Smith, C. A., Herzog, M. P., Topping, B. R., Shellenbarger, G. G., Kuwabara, J. S. and Mruz, E., 2015. Unintended consequences of management actions in salt pond restoration: Cascading effects in trophic interactions. *PLoS One*, 10 (6), e0119345.

Targońska, K., Kupren, K., Palińska-żarska, K., Mamcarz, A., Kujawa, R., Skrzypczak, A., Furgała-Selezniow, G., Czarkowski, T. K., Hakuć-Błażowska, A. and Kucharczyk, D., 2014. Influence of temperature during four following spawning seasons on the spawning effectiveness of common bream, *Abramis brama* (L.) under natural and controlled conditions. *Journal of Thermal Biology,* 39, 17-23.

Tarkan, A. S. and Vilizzi, L., 2015. Patterns, latitudinal clines and countergradient variation in the growth of roach *Rutilus rutilus* (Cyprinidae) in its Eurasian area of distribution. *Reviews in Fish Biology and Fisheries*, 25 (4), 587-602.

Taylor, M. D., van der Meulen, D. E., Brodie, S., Cadiou, G. and Knott, N. A., 2018. Applying acoustic telemetry to understand contaminant exposure and bioaccumulation patterns in mobile fishes. *Science of The Total Environment*, 625, 344-354.

Taylor, M. K. and Cooke, S. J., 2012. Meta-analyses of the effects of river flow on fish movement and activity. *Environmental Reviews*, 20 (4), 211-219.

Therneau, T. M., 2020. *A Package for Survival Analysis in R* [online]. R package version 3.1-12. Available from: https://CRAN.R-project.org/package=survival

Therneau, T. M. and Grambsch, P. M., 2000. *Modelling survival data: extending the Cox model*. New York, USA: Springer-Verlag.

Thieurmel, B. and Elmarhraoui, A., 2019. suncalc: Compute Sun Position, Sunlight Phases, Moon Position and Lunar Phase. *R package version 0.5.0*, https://CRAN.R-project.org/package=suncalc.

Thompson, T. Q., Bellinger, M. R., O'Rourke, S. M., Prince, D. J., Stevenson, A. E., Rodrigues, A. T., Sloat, M. R., Speller, C. F., Yang, D. Y. and Butler, V. L., 2019. Anthropogenic habitat alteration leads to rapid loss of adaptive variation and restoration potential in wild salmon populations. *Proceedings of the National Academy of Sciences*, 116 (1), 177-186.

Thorstad, E. B., Økland, F., Westerberg, H., Aarestrup, K. and Metcalfe, J. D., 2013. Evaluation of surgical implantation of electronic tags in European eel and effects of different suture materials. *Marine and Freshwater Research*, 64 (4), 324-331.

Tomlinson, M., Perrow, M., Hoare, D., Pitt, J., Johnson, S., Wilson, C. and Alborough, D., 2002. Restoration of Ormesby Broad through biomanipulation: ecological, technical and sociological issues. *In:* Cowx, I. G., ed. *Management and Ecology of Lake and Reservoir Fisheries.* John Wiley & Sons, 184-202.

Tomlinson, M. L., Perrow, M. and Harwood, A. J., 2010. *Connecting wetlands: Assessment of the use of wetlands by fish and guidelines for fish management in wetland in the Broads*. ECON Consultancy on behalf of Broads Authority.

Torniainen, J., Lensu, A., Vuorinen, P. J., Sonninen, E., Keinänen, M., Jones, R. I., Patterson, W. P. and Kiljunen, M., 2017. Oxygen and carbon isoscapes for the Baltic Sea: Testing their applicability in fish migration studies. *Ecology and Evolution*, 7 (7), 2255-2267.

Trekels, H., Van de Meutter, F. and Stoks, R., 2011. Habitat isolation shapes the recovery of aquatic insect communities from a pesticide pulse. *Journal of Applied Ecology*, 48 (6), 1480-1489.

Trueman, C. N., MacKenzie, K. and Palmer, M., 2012. Identifying migrations in marine fishes through stable-isotope analysis. *Journal of Fish Biology*, 81 (2), 826-847.

Tucker, M. A., Böhning-Gaese, K., Fagan, W. F., Fryxell, J. M., Van Moorter, B. and al., e., 2018. Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science*, 359 (6374), 466-469.

Tummers, J. S., Winter, E., Silva, S., O'Brien, P., Jang, M.-H. and Lucas, M. C., 2016. Evaluating the effectiveness of a Larinier super active baffle fish pass for European river lamprey *Lampetra fluviatilis* before and after modification with wall-mounted studded tiles. *Ecological Engineering*, 91, 183-194.

Turbek, S. P., Scordato, E. S. and Safran, R. J., 2018. The role of seasonal migration in population divergence and reproductive isolation. *Trends in Ecology & Evolution*, 33 (3), 164-175.

Udyawer, V., Dwyer, R. G., Hoenner, X., Babcock, R. C., Brodie, S., Campbell, H. A., Harcourt, R. G., Huveneers, C., Jaine, F. R. and Simpfendorfer, C. A., 2018. A standardised framework for analysing animal detections from automated tracking arrays. *Animal Biotelemetry*, 6 (1), 1-14.

Vaida, F. and Blanchard, S., 2005. Conditional Akaike information for mixed-effects models. *Biometrika*, 92 (2), 351-370.

Van De Bund, W. J. and Van Donk, E., 2002. Short-term and long-term effects of zooplanktivorous fish removal in a shallow lake: a synthesis of 15 years of data from Lake Zwemlust. *Freshwater Biology*, 47 (12), 2380-2387.

Van Puijenbroek, P. J., Buijse, A. D., Kraak, M. H. and Verdonschot, P. F., 2019. Species and river specific effects of river fragmentation on European anadromous fish species. *River Research and Applications*, 35 (1), 68-77.

Vander Zanden, H. B., Nelson, D. M., Wunder, M. B., Conkling, T. J. and Katzner, T., 2018. Application of isoscapes to determine geographic origin of terrestrial wildlife for conservation and management. *Biological Conservation*, 228, 268-280.

Vander Zanden, H. B., Tucker, A. D., Hart, K. M., Lamont, M. M., Fujisaki, I., Addison, D. S., Mansfield, K. L., Phillips, K. F., Wunder, M. B. and Bowen, G. J., 2015a. Determining origin in a migratory marine vertebrate: a novel method to integrate stable isotopes and satellite tracking. *Ecological Applications*, 25 (2), 320-335.

Vander Zanden, M. J., Clayton, M. K., Moody, E. K., Solomon, C. T. and Weidel, B. C., 2015b. Stable isotope turnover and half-life in animal tissues: A literature synthesis. *Plos One*, 10 (1), 1-16.

Vergeynst, J., Vanwyck, T., Baeyens, R., De Mulder, T., Nopens, I., Mouton, A. and Pauwels, I., 2020. Acoustic positioning in a reflective environment: going beyond point-by-point algorithms. *Animal Biotelemetry*, 8, 1-17.

Villegas-Ríos, D., Freitas, C., Moland, E., Huneide Thorbjørnsen, S. and Olsen, E. M., 2020. Inferring individual fate from aquatic acoustic telemetry data. *Methods in Ecology and Evolution*, doi: 10.1111/2041-1210X.13446

Voigt, C. C., Popa-Lisseanu, A. G., Niermann, I. and Kramer-Schadt, S., 2012. The catchment area of wind farms for European bats: a plea for international regulations. *Biological Conservation*, 153, 80-86.

Voigt, M. B., Hackenbroich, C., Krüger, H.-H., Liebau, A. and Esser, K.-H., 2019. The in-air auditory thresholds of the eurasian otter (*Lutra lutra*, L. 1758) as determined by auditory brainstem responses. *Hearing Research*, 381, 107774.

Volta, P., Jeppesen, E., Leoni, B., Campi, B., Sala, P., Garibaldi, L., Lauridsen, T. L. and Winfield, I. J., 2013. Recent invasion by a non-native cyprinid (common bream *Abramis brama*) is followed by major changes in the ecological quality of a shallow lake in southern Europe. *Biological Invasions*, 15 (9), 2065-2079.

Wallace, A. A., Hollander, D. J. and Peebles, E. B., 2014. Stable isotopes in fish eye lenses as potential recorders of trophic and geographic history. *PLoS ONE*, 9 (10).

Walsh, M. G., Bjorgo, K. A. and Isely, J. J., 2000. Effects of implantation method and temperature on mortality and loss of simulated transmitters in hybrid striped bass. *Transactions of the American Fisheries Society*, 129 (2), 539-544.

Ward, A. J., Kent, M. I. and Webster, M. M., 2020. Social recognition and social attraction in group-living fishes. *Frontiers in Ecology and Evolution*, 8, https://doi.org/10.3389/fevo.2020.00015.

Warner, R. R., 1988. Traditionality of mating-site preferences in a coral reef fish. *Nature*, 335 (6192), 719-721.

Weinz, A. A., 2020. *Acoustic telemetry in freshwater habitats: the influence of macrophytes on acoustic transmitter detection efficiency and identifying predation using novel transmitters*. Vol. Master of Science. University of Windsor Electronic Theses and Dissertations. 8327: Great Lakes Institute for Environmental Research.

Welch, D., Batten, S. and Ward, B., 2007. Growth, survival, and tag retention of steelhead trout (*O. mykiss*) surgically implanted with dummy acoustic tags. *Developments in Fish Telemetry*. Springer, 289-299.

Weston, N., Goosem, M., Marsh, H., Cohen, M. and Wilson, R., 2011. Using canopy bridges to link habitat for arboreal mammals: successful trials in the Wet Tropics of Queensland. *Australian Mammalogy*, 33 (1), 93-105.

Whelan, K., 1983. Migratory patterns of bream *Abramis brama* L. shoals in the River Suck System. *Irish Fisheries Investigations, Series A*, 23, 11-15.

Whitlock, S. L., Campbell, M. R., Quist, M. C. and Dux, A. M., 2018. Using genetic and phenotypic comparisons to evaluate apparent segregation among kokanee spawning groups. *Transactions of the American Fisheries Society*, 147 (1), 43-60.

Whitty, J. M., Morgan, D. L., Peverell, S. C., Thorburn, D. C. and Beatty, S. J., 2009. Ontogenetic depth partitioning by juvenile freshwater sawfish (*Pristis microdon*: Pristidae) in a riverine environment. *Marine and Freshwater Research*, 60 (4), 306-316.

Whoriskey, K., Martins, E. G., Auger-Méthé, M., Gutowsky, L. F., Lennox, R. J., Cooke, S. J., Power, M. and Mills Flemming, J., 2019. Current and emerging statistical techniques for aquatic telemetry data: A guide to analysing spatially discrete animal detections. *Methods in Ecology and Evolution*, 10 (7), 935-948.

Wilson, A. D., Binder, T. R., McGrath, K. P., Cooke, S. J. and Godin, J.-G. J., 2011. Capture technique and fish personality: angling targets timid bluegill sunfish, *Lepomis macrochirus*. *Canadian Journal of Fisheries and Aquatic Sciences*, 68 (5), 749-757.

Wilson, R. P. and McMahon, C. R., 2006. Measuring devices on wild animals: what constitutes acceptable practice? *Frontiers in Ecology and the Environment*, 4 (3), 147-154.

Winter, E., Tummers, J., Aarestrup, K., Baktoft, H. and Lucas, M., 2016. Investigating the phenology of seaward migration of juvenile brown trout (*Salmo trutta*) in two European populations. *Hydrobiologia*, 775 (1), 139-151.

Winter, E. R., Nolan, E. T., Busst, G. M. and Britton, J. R., 2019. Estimating stable isotope turnover rates of epidermal mucus and dorsal muscle for an omnivorous fish using a diet-switch experiment. *Hydrobiologia*, 828 (1), 245-258.

Wood, S. and Scheipl, F., 2020. gamm4: Generalized Additive Mixed Models using 'mgcv' and 'lme4'. *R package version 0.2-6*, https://CRAN.R-project.org/package=gamm4.

Wysujack, K., Greenberg, L., Bergman, E. and Olsson, I., 2009. The role of the environment in partial migration: food availability affects the adoption of a migratory tactic in brown trout *Salmo trutta*. *Ecology of Freshwater Fish*, 18 (1), 52-59.

Yasuda, T., Nagano, N., Kitano, H., Ohga, H., Sakai, T., Ohshimo, S. and Matsuyama, M., 2015. Tag attachment success can be temperature dependent: a case study of the chub mackerel *Scomber japonicus*. *Animal Biotelemetry*, 3 (1), 48.

Žák, J., Prchalova, M., Šmejkal, M., Blabolil, P., Vašek, M., Matěna, J., Říha, M., Peterka, J., Seďa, J. and Kubečka, J., 2020. Sexual segregation in European cyprinids: consequence of response to predation risk influenced by sexual size dimorphism. *Hydrobiologia*, 847 (6), 1439-1451.

Zambrano, L., Scheffer, M. and Martínez-Ramos, M., 2001. Catastrophic response of lakes to benthivorous fish introduction. *Oikos*, 94 (2), 344-350.

Zarfl, C., Lumsdon, A. E., Berlekamp, J., Tydecks, L. and Tockner, K., 2015. A global boom in hydropower dam construction. *Aquatic Sciences*, 77 (1), 161-170.

Zydlewski, G., Haro, A., Whalen, K. and McCormick, S., 2001. Performance of stationary and portable passive transponder detection systems for monitoring of fish movements. *Journal of Fish Biology*, 58 (5), 1471-1475.

Appendices

Appendix 1: High temporal and spatial variability in the detection efficiency of acoustic telemetry receivers in a connected wetland system

Table A1.1: Combinations of covariates tested in generalised linear mixed models predicting daily detection efficiency of acoustic receivers. Models are ordered according to ΔAIC values.

Model	ΔAIC
~ Temperature + Precipitation	0
~ Temperature + Precipitation + Noise	1.96
~ Temperature	10.17
~ Temperature + Noise	12.14
~ Precipitation + Noise	225.02
~ Precipitation	229.94
~ Noise	231.68
Null model	236.73
~ Wind	237.91

Table A1.2: Combinations of covariates tested in linear mixed models predicting detection range of acoustic receivers. Models are ordered according to ΔAIC values.

Model	ΔAIC
~ Transparency + Wind	0
~ Transparency	5.62
~ Temperature + Wind	9.17
~ Conductivity + Wind	10.08
~ Temperature	14.95
~ Conductivity	16.28
~ Wind	19.30
Null model	25.57

Appendix 2: Predicting the factors influencing the inter- and intra-specific survival rates of riverine fishes implanted with acoustic transmitters

Table A2.1. Combinations of covariates tested in Cox Proportional Hazard models predicting bream (a, b) and pike (c, d) survival. Models are ordered according to ΔAIC values. NA values represent model non-convergence. Models incorporating and comparing the effect of fish sex were performed on subsets of data (b, d).

Model covariates	ΔAIC	d.f.
a) Bream (complete dataset)		
~ pspline(Tagging date) + pspline(Day of year) + Year	0.00	8.06
~ pspline(Tagging date) + pspline(Day of year)	0.85	7.86
~ pspline(Tagging date) + Temperature + Year	30.40	4.79
~ pspline(Tagging date) + Temperature	31.07	4.29
~ pspline(Day of year) + Sampling location + Year	34.86	8.01
~ pspline(Day of year) + Sampling location	40.14	7.33
~ pspline(Tagging date) + Year	57.49	4.28
~ pspline(Tagging date)	64.79	3.10
~ Sampling location + Temperature + Year	67.28	5.00
~ Sampling location + Temperature	68.99	4.00
~ pspline(Day of year) + Fish length	69.15	7.39
~ pspline(Day of year) + Fish length + Year	70.26	7.30
~ pspline(Day of year)	71.79	6.85
~ Sampling location + Year	72.87	4.00
~ pspline(Day of year) + Year	72.89	7.77
~ Sampling location	85.05	3.00
~ Fish length + Temperature	100.42	2.00
~ Fish length + Temperature + Year	101.33	3.00
~ Fish length + Year	102.84	2.00
~ Temperature	103.01	1.00

(continued overleaf)

(Table A2.1 continued)

Model covariates	ΔAIC	d.f.
~ Temperature + Year	104.01	2.00
~ Tagging date	104.14	1.00
~ Day of year	105.19	1.00
~ Year	105.69	1.00
~ Fish length	105.69	1.00
Null model	108.31	0.00
b) Bream (subset of data)		
Null model	0.00	0.00
~ Sex	1.75	1.00
c) Pike (complete dataset)		
~ pspline(Day of year)	0.00	3.71
Null model	5.27	0.00
~ Day of year	7.26	1.00
~ Fish length	7.27	1.00
~ Tagging date	7.27	1.00
~ pspline(Tagging date)	7.27	1.00
~ Sampling location	10.35	3.00
~ Year	NA	NA
d) Pike (subset of data)		
~ pspline(Day of year) + Sex	0.00	4.77
~ pspline(Day of year)	4.36	3.70
~ Sex	5.47	1.00
Null model	9.96	0.00

Table A2.2. Coefficient estimates (β ± robust SE) for relevant predictors retained in the alternative CPH model (ΔAIC = 0.85) predicting bream survival.

Parameter	β	Wald's χ^2	d.f.	p
Tagging date (linear)	-0.00006 ± 0.00114	0.01	1.00	0.93
Tagging date (nonlinear)		84.14	2.77	< 0.0001
Day of year (linear)	-0.0027 ± 0.0016	7.18	1.00	0.0074
Day of year (nonlinear)		138.10	3.09	< 0.0001

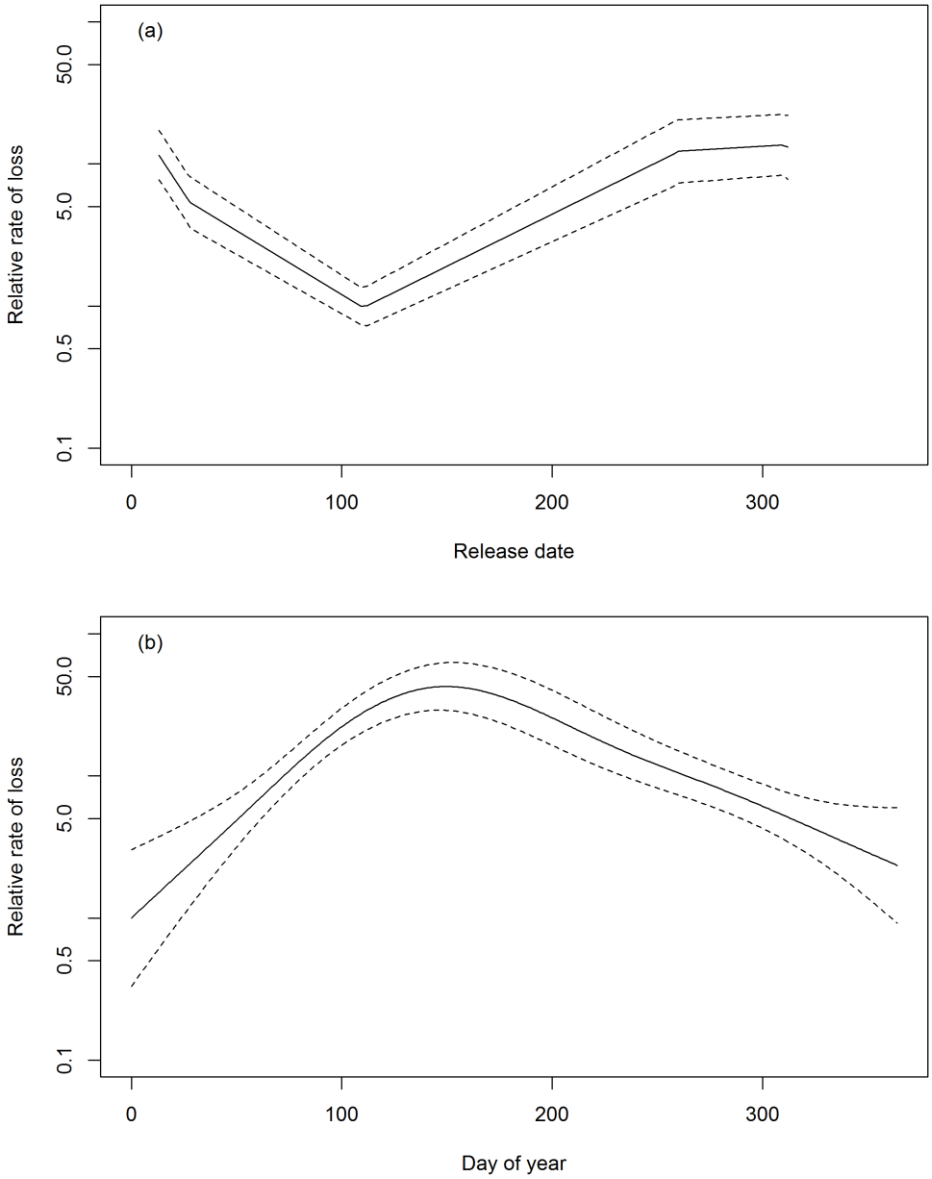

Figure A2.1. Nonlinear effects ('p-spline' smoothing) of tagging date (a) and day of year (b) on the rate of loss of bream from the acoustic telemetry study according to the alternative CPH model (ΔAIC = 0.85). Hazards are relative to Day = 109 (a) and Day = 0 (b). X-axes represent time in Julian days.

Appendix 3: Dual-isotope isoscapes for predicting the scale of fish movements in lowland rivers

Table A3.1: Details of acoustically tagged common bream according to sample site and tracking duration.

Tag ID	Sample site	Length (FL) at tagging (mm)	$\delta^{13}C$ at tagging (‰)	$\delta^{15}N$ at tagging (‰)	Duration of tracking (days)
26118	4	321	-25.02	14.85	12
4997	7	421	-27.75	17.52	49
26119	4	354	-28.64	17.76	119
4995	8	383	-27.79	18.71	176
26112	7	395	-28.77	16.98	179
26120	7	468	-28.51	16.51	184
26117	4	401	-27.21	16.39	196
4992	7	415	-27.84	16.79	202
26122	4	376	-26.56	17.71	213
26128	4	388	-27.18	17.38	215
26123	4	408	-25.21	15.96	216
26124*	4	377	-26.83	18.15	286
5005*	8	403	-29.33	16.16	364
26111*	4	503	-26.92	16.09	365
4991*	7	437	-29.08	16.57	365
4993*	7	491	-29.63	17.86	365
26113*	7	461	-27.68	16.46	365
4985*	8	368	-28.58	17.85	365
4987*	8	438	-28.90	17.45	365

* Selected for analysis

Appendix 4: Movements of common bream *Abramis brama* in a highly-connected, lowland wetland reveal spatially discrete sub-populations with diverse migration strategies

Table A4.1: Univariate CTMMs performed on a reduced dataset (11 bream removed due to unreliable sex determination), ordered by Akaike Information Criterion (AIC) values. NA values signify non-convergence.

Model	ΔAIC
~ Length	0.00
~ Season	39.52
~ Light	223.10
~ Conductivity	235.32
~ Temperature	236.26
~ Tidal phase	245.66
~ Sex	254.42
~ Tidal level	257.61
~ Year	258.75
~ Null	266.88
~ Group	NA

Appendix 5: Acoustic telemetry reveals strong spatial preferences and mixing during successive spawning periods in a partially migratory common bream population

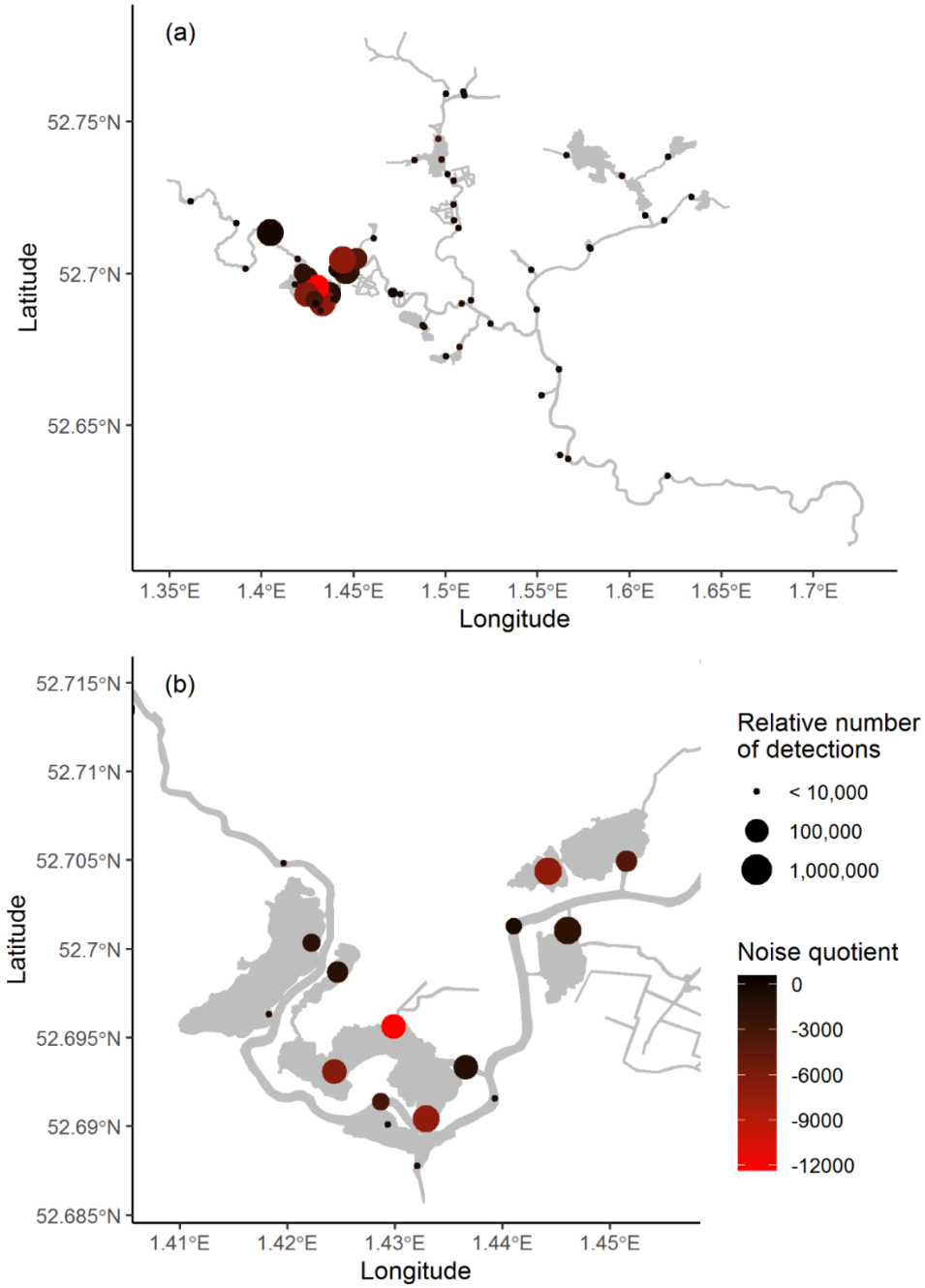

Figure A5.1: Total number of detections of 'resident' bream at each acoustic receiver during the 2019 spawning period (a) across the entire study area and (b) in a section of the Upper Bure reach. Detections are scaled relative to the detection area of each receiver when detection range = 200 m. Points are coloured according to the mean daily noise quotient, with values < 0 indicating interference by tag collisions.

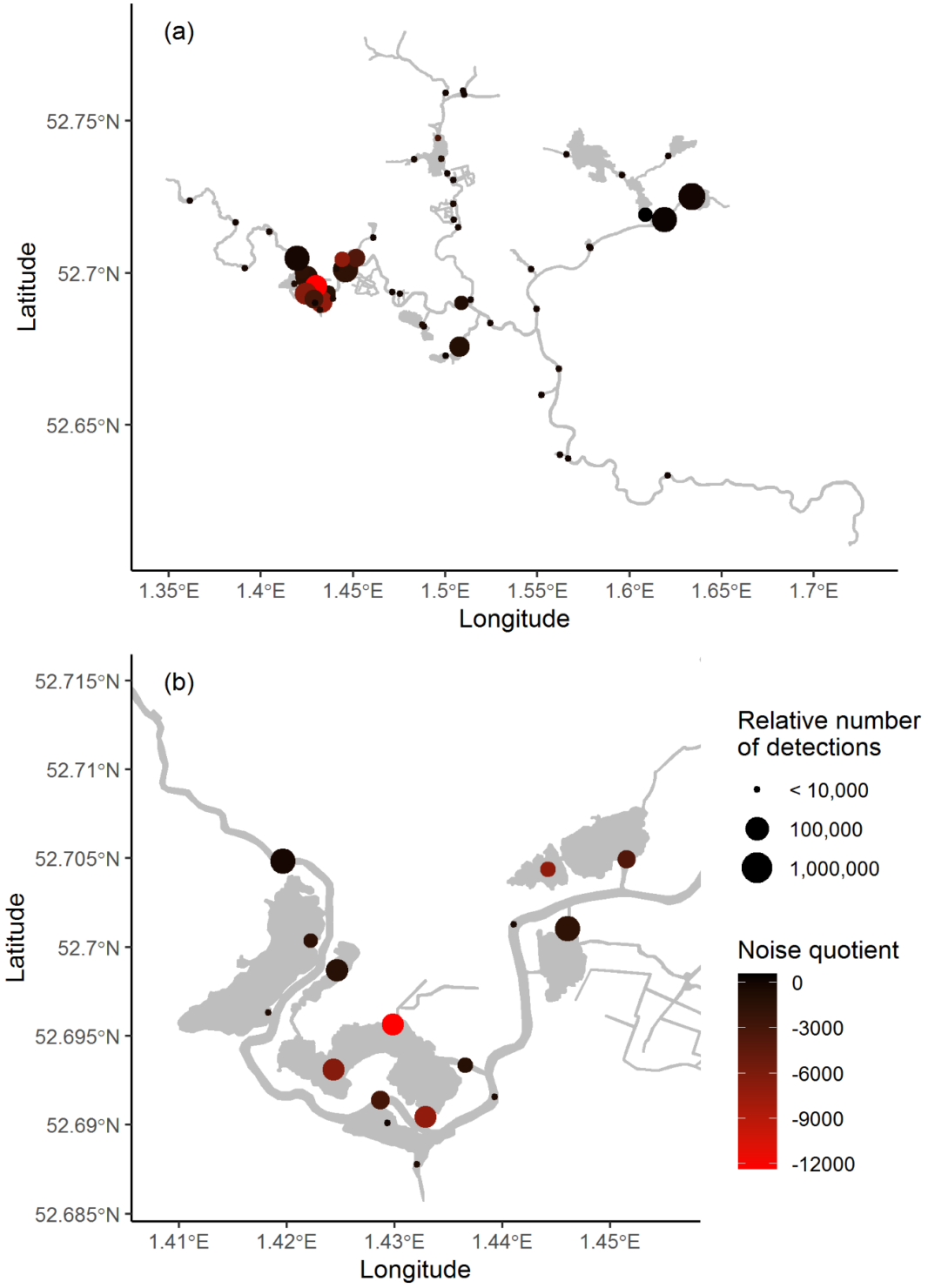

Figure A5.2: Total number of detections of 'migrant' bream at each acoustic receiver during the 2019 spawning period (a) across the entire study area and (b) in a section of the Upper Bure reach. Detections are scaled relative to the detection area of each receiver when detection range = 200 m. Points are coloured according to the mean daily noise quotient, with values < 0 indicating interference by tag collisions.

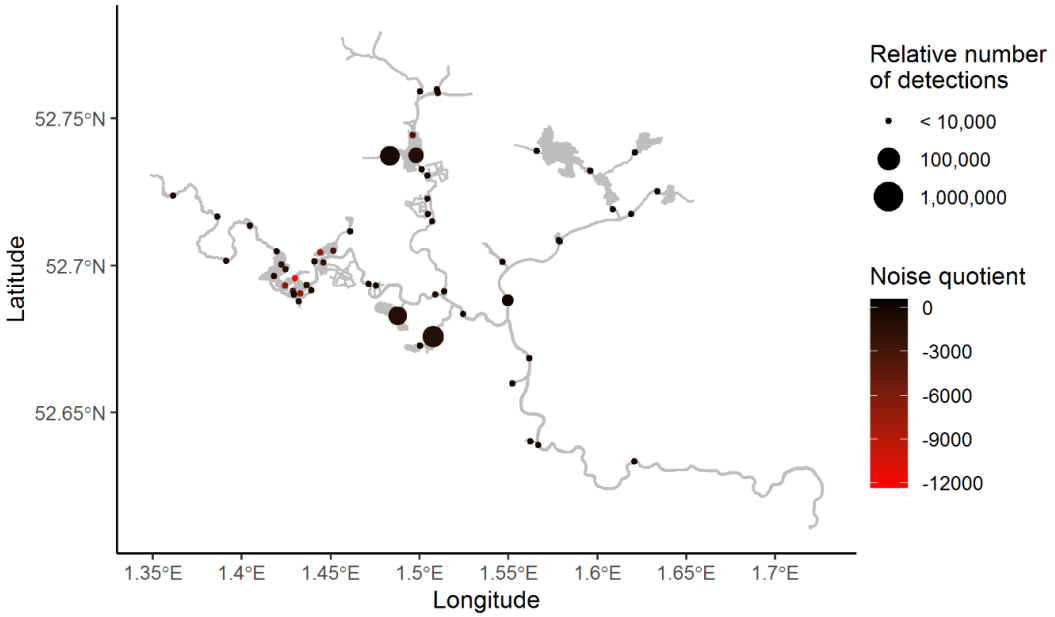

Figure A5.3: Total number of detections of bream classified 'other' (n = 13) at each acoustic receiver across the study area during the 2019 spawning period. Detections are scaled relative to the detection area of each receiver when detection range = 200 m. Points are coloured according to the mean daily noise quotient, with values < 0 indicating interference by tag collisions.